THE QUARTERLY REVIEW *of* BIOLOGY

VOLUME 20

1945

Published by

THE WILLIAMS & WILKINS COMPANY
BALTIMORE
U. S. A.

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

Chester C. Corbin Library Fund
Bound Aug. 1946

THE QUARTERLY REVIEW OF BIOLOGY

FOUNDED BY RAYMOND PEARL

B. H. WILLIER, *Editor*
The Johns Hopkins University

H. BENTLEY GLASS
Assistant Editor

MAUD DEWITT PEARL
Assistant Editor

ADVISORY BOARD

ANATOMY	LEWIS H. WEED	*The Johns Hopkins University*
ANTHROPOLOGY	A. L. KROEBER	*University of California*
BEHAVIOR AND COMPARATIVE PSYCHOLOGY	K. S. LASHLEY	*Harvard University*
BOTANY	IRVING W. BAILEY	*Harvard University*
CYTOLOGY	CHARLES W. METZ	*University of Pennsylvania*
ECOLOGY	THOMAS PARK	*University of Chicago*
EMBRYOLOGY	E. G. CONKLIN	*Princeton University*
EXPERIMENTAL MORPHOLOGY	ROSS G. HARRISON	*Yale University*
GENERAL PHYSIOLOGY	G. H. PARKER	*Harvard University*
	F. O. SCHMITT	*Massachusetts Institute of Technology*
GENETICS	R. A. EMERSON	*Cornell University*
	T. H. MORGAN	*California Institute of Technology*
GEOGRAPHICAL DISTRIBUTION AND TAXONOMY	ALEXANDER G. RUTHVEN	*University of Michigan*
PALEONTOLOGY	JOHN C. MERRIAM	*Carnegie Institution*
	ALFRED S. ROMER	*Harvard University*
ZOOLOGY	FRANK R. LILLIE	*University of Chicago*

QH
301
F261
v.20

CONTENTS

No. 1, March, 1945

Current Status of Our Knowledge of the Golgi Apparatus in the Animal Cell. . *Hope Hibbard* 1
The Effects of Changes in Chromosome Number on Amphibian Development. *G. Fankhauser* 20
New Biological Books:
Reviews and Brief Notices 79

No. 2, June, 1945

Physiological Competition as A Regulatory Mechanism in Morphogenesis. . . *S. Spiegelman* 121
Mimetic Polymorphism, A Controversial Chapter of Darwinism. . . . *Richard B. Goldschmidt* 147
New Biological Books:
Darwin and Social Theory in America ..... *Raymond P. Hawes* 165
Reviews and Brief Notices 167

No. 3, September, 1945

Mimetic Polymorphism, A Controversial Chapter of Darwinism (Concluded)
Richard B. Goldschmidt 205
The Evolution of Male Haploidy ..... *P. W. Whiting* 231
New Biological Books:
Evolution: A Synthesis of Paleontology and Genetics ..... *Bentley Glass* 261
Reviews and Brief Notices 263

No. 4, December, 1945

The Problem of Central Nervous Reorganization after Nerve Regeneration and Muscle Transposition ..... *R. W. Sperry* 311
New Biological Books:
What Is Life? and What Is Truth? ..... *Max Delbrück* 370
Reviews and Brief Notices 372
Index 419

VOL. 20, NO. 1 March, 1945

THE QUARTERLY REVIEW of BIOLOGY

CURRENT STATUS OF OUR KNOWLEDGE OF THE GOLGI APPARATUS IN THE ANIMAL CELL

By HOPE HIBBARD
Oberlin College

INTRODUCTION

THERE have been several summaries of work on the Golgi apparatus of recent date, notably that of Kirkman and Severinghaus (1938), that of Hirsch (1939a) and that of Bourne (1942). They present somewhat different points of view, and this, together with the fact that a number of highly important papers have since been published, suggests this additional review.

Prior to the time of the publication of the paper by Golgi from which stems the enormous volume of literature on the subject, there were at least ten papers in which mention or figures of cellular components were included that many later investigators have thought might have been called Golgi apparatus had the papers appeared at later dates. From Golgi's publication in 1898 to the present time somewhat over two thousand descriptions and interpretations of this structure have appeared. Golgi himself lived for many years in scientific seclusion, and one wonders what his thoughts may have been regarding all the furor of discussion of the structures bearing his name.

An analysis of the numbers of papers appearing year by year shows a slow increase in interest in the subject for the first twenty years, then, beginning in 1920, a sharper increase reaching a peak in 1928–30, followed by a sharp decrease to the present. Some of the most recent falling off of publication must be ascribed to war conditions, primarily because research is not going on as in peace time and also because many foreign papers are not available. But the trend of decreasing numbers of papers year by year was well started before the outbreak of the present war. A graphic summary of these data may be seen in figure 1. The titles counted before 1938 correspond for the most part to those listed in the extremely full bibliography included in the book by Hirsch. The list includes a few papers on plant cytology, but no effort has been made to search the botanical literature.

During the first half of the period from the discovery of the Golgi apparatus to the present, investigators were primarily concerned with morphological descriptions of it in all sorts of cell types. Just before and during the peak years some of the very active workers were Beams, Bowen, Gatenby, Guilliermond, Hirschler, Ludford, Nassonov, and Parat,—names which students of cytology will recognize as catalysing agents in this type of research. Through these peak years, and since, questions as to the nature of the apparatus and its physiological significance have been uppermost. Does the falling off in the number of papers indicate an increasing lack of interest, or the general acceptance of a solution? May we expect that the curve will fall entirely and that this problem will retire into the limbo of history as one of the amazing phenomena in the annals of controversial scientific literature?

It is necessary at the outset to admit that there does not seem to be much agreement as to the nature and functioning of the Golgi apparatus. To quote from MacLennan (1939) as to the situa-

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

tion in Protozoa, "The term Golgi body, being based upon non-specific criteria . . . includes a heterogeneous group of structures, including scattered endoplasmic granules and granules associated with contractile vacuoles or fused to form heavy and permanent vacuolar membranes. . . . Since the impregnation reactions themselves do not reveal homologies which must be based on composition and function, the retention of the term Golgi body is merely a convenience to bridge the change from reliance on the non-specific osmic techniques to reliance upon cytochemical and physiological criteria." There is the crux of the matter. In all

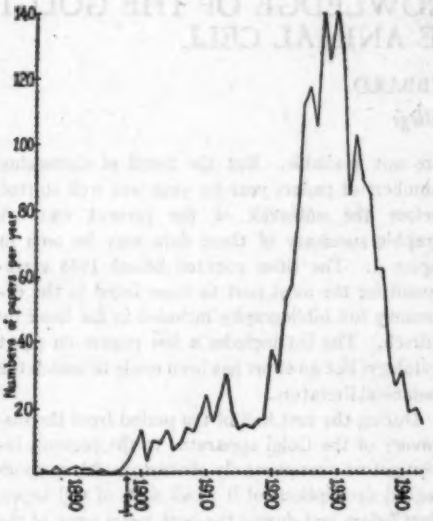

FIG. 1. GRAPH SHOWING DISTRIBUTION OF PAPERS ON THE GOLGI APPARATUS OVER THE YEARS
2074 titles are represented

the years during which cytologists have been discussing the Golgi apparatus, the basic criterion of identification has been impregnation with osmic acid or silver nitrate, neither of which is specific.

The picture is complicated for the general reader by the abundance of terms used by individual workers for slight variations in observed details. The tendency to coin new names did not stop with early workers using a new technique to demonstrate something hitherto overlooked, but it continues down to the present. Thus Hirsch (1939a) is able to list in a table with dates, authors, and definitions, one hundred and twenty names for all or for parts of the Golgi apparatus. And Hirsch attempts to re-interpret all these names in terms of his own particular categories. On the other hand, Salazar (1942) has translated Hirsch's names as well as many previously invented by earlier workers into "Golgi apparatus" and "para-Golgi apparatus"; and so on.

Some of the questions most frequently asked as to the Golgi apparatus are: (1) Does it exist as figured or is it an artefact? (2) Is it a permanent structure or does it sometimes disappear? (3) Is its form significant? (4) What are its physical characteristics? (5) What is it, chemically speaking? (6) What are its functions? These questions will be discussed, in the light of what has been published during the last six years, in the following sections.

ARTEFACT?

Probably no cytologist who ever worked upon this problem would deny the existence of something special that blackens with osmic acid and silver nitrate. It is quite obvious that the entire cell does not blacken uniformly. The suggestion of an artefact implies only a possible displacement of materials in the living cell during the preparation for examination, or changes in form, so that the resulting "apparatus" is somewhat different from the special materials or structures that were present in the living and functioning cell at first. Worley and Worley (1943) and Worley (1943b) demonstrated the high susceptibility of cytoplasmic inclusions to changes in form or displacement or both, in embryonic and larval cells of nudibranch molluscs, when there is variation in hydrostatic pressure, as in drying or during fixation. Thus vesicles may be ruptured, and their contents may spring to the surfaces of nearby fatty or albuminous yolk, or may form batonnets in the cytoplasm. Moreover, both intact and ruptured vesicles may be seen in the same living cell, a fact which might lead to erroneous descriptions of more than one type of cytoplasmic inclusion in fixed material. Worley and Worley assume that these vesicles are the Golgi apparatus. They appear as granules, droplets, vesicles, or masses when alive; after fixation artefacts may appear as rings, plates, cups, discs, etc. Similar form changes may be simulated in fresh material by creating shrinkage, comparable to that produced by fixatives, with hypertonic salt solutions.

At an earlier date, Carter (1928) described in the veliger of the nudibranch, *Aeolidia*, a variety of granules in the living cells and among them many with Janus green stained crescents attached.

Figure 19 by Worley (1944a) and figure 7 by Carter (1928) show almost identical bodies,—Golgi bodies, according to Worley, and reserve food vacuoles with mitochondria attached, according to Carter.

Direct proof of the fidelity of the fixed picture by observation of the structure in the same form in the living cell has not been accomplished generally. Although Kirkman and Severinghaus state that "the time-honored belief that Golgi materials cannot be seen in living cells is no longer pertinent," a statement with which Hirsch (1939) is in agreement, they cast doubt on the identity of much that has been described as Golgi material in living cells, such as vacuoles or fat globules. While Hirsch claims agreement with the statement of Kirkman and Severinghaus, he admits that he is unable to see the Golgi substance in the Golgi field in unstained preparations of gland cells. Since Hirsch is responsible for much painstaking and accurate preparation and observation of the living pancreas cell in the mouse, where he kept the circulation about the acinus intact during the whole period of observation and did not in any way dissociate the cells, his failure to see a network in that area where he could impregnate it constitutes an important observation. The writer was unable to see in the living proventriculus or gizzard of the chick anything resembling the enormous and easily demonstrated black apparatus of appropriately fixed tissues. This has been the experience of most cytologists in attempting to discern the typical network in somatic cells of vertebrates.

Although the authors quoted above doubted the correctness of interpreting things like fat droplets or vacuoles as Golgi bodies, they assumed as a matter of course that the Golgi bodies in male germ cells are correctly identified and named. These, unlike those in Hirsch's gland cells, are clearly visible alive, both unstained and stained vitally by Janus green, and from observations of this sort comes most of the evidence that the Golgi apparatus may be seen in living cells. Filhol (1938), it is true, found similar bodies which were visible in all living unstained cells observed in many parts of the reproductive apparatus of pulmonates, bodies which also stained with Janus green. His interpretation of these will be discussed further on (p. 4). These differences alone would seem to cast some doubt on the identity of the Golgi networks and the discrete dictyosomes found in male germ cells. Kirkman and Severinghaus (1938), however, conclude that the latter are actually Golgi material like that of the somatic cells, as follows: "This evidence" [the secretion of the acrosome by Golgi bodies] "is so clear-cut in many instances that the only way of getting around it is by claiming, with the upholders of the vacuome hypothesis, that the dictyosomes of male germ cells do not represent Golgi material, but, as stated by Wilson and Pollister (1937) this claim can no longer be supported in the face of conclusive evidence that 'there is no substantial difference between the Golgi bodies of the germ cells and those of other tissue cells'" (pp. 85, 86). It may be noted that

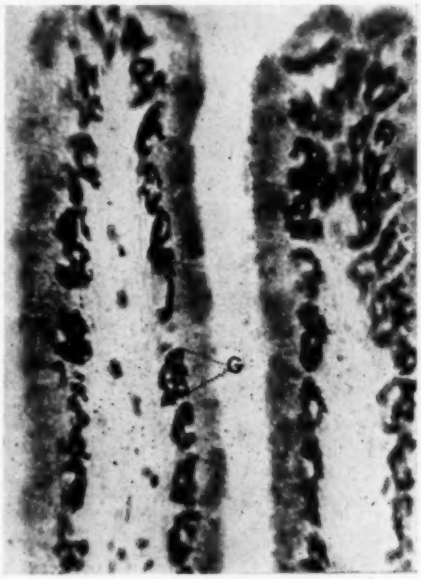

FIG. 2. PHOTOMICROGRAPH OF CELLS LINING THE CHICKEN GIZZARD IMPREGNATED BY THE DA FANO METHOD AND UNSTAINED
G—the Golgi apparatus of a single cell (photographed by R. S. McEwen)

the phrase quoted from Wilson and Pollister is taken from a complete sentence which is qualified as follows: "The observation of their film-like, frequently cup-like, shape is in agreement with the findings of many other cytologists, not only in the germ cells but also in the tissue cells, and *in this respect* the findings on *Centrurus* and *Centruroides* support the contention that there is no substantial difference between the Golgi bodies of the germ cells and those of other tissue cells." (pp. 415, 416, italics mine.) The phrase in its context is far less dogmatic than would appear from the first quotation.

It is quite true that most cytologists currently publishing tacitly assume the dictyosome to be intrinsically the same as any other Golgi apparatus, and they tend to generalize any observation of a special case. Thus the Golgi apparatus, in a broad sense, is assumed to be largely lipoidal because the dictyosomes are lipoidal, or it is said that the Golgi apparatus can be seen in normal living cells primarily because the dictyosome may be seen under those conditions, etc. In Hirsch's various extensive publications such tacit assumptions are evident, and he refers to the Golgi system in the male germ cell as an excellent example of a "mono-system" (see p. 7).

While this review is primarily concerned with current ideas and the publications of the last six years, the discussion of the dictyosome cannot be concluded without a reference to the work of Parat (1938), published a year before his death. Though few cytologists have ever supported his interpretation of this problem, the dilemma which he pointed out is still evident in current findings. The facts that the dictyosomes have so frequently been observed in living cells, while the network in somatic cells has not; that they stain with Janus green in the one case but not in the other; that the dictyosomes have been stained with Sudan III, indicating their high lipoid content and that they are stainable with hematoxylin or acid fuchsin while the network is not [though Bachman (1939) described in the guinea pig adrenal cortex an extensive hematoxylin-staining body, after Bouin fixation, which suggests a Golgi net, but which bears no resemblance in form or position to the Golgi apparatus described by Bennett (1940) in the cat]; that the dictyosomes have a more constant morphology than the net and are less deformed by centrifuging;—all these differences must be weighed against the morphological evidence for a similar relation to secretory activity and the fact that both may be blackened by osmic acid. Parat concluded from such comparisons that the dictyosomes had much more in common with chondriosomes than with the heavily blackened masses in gland cells, for instance, and there are several recent publications in which strong reliance is placed upon his conclusions, in work upon other than germ cells. Among them are Filhol and Garrault (1938) on nidamental glands, Feyel (1939) on the guinea pig hypophysis, Dehorne (1938, 1939) on parapodial glands in annelids, where typical filamentous mitochondria were observed to become pachynetic and grow into the duplex Golgi bodies. Also Filhol (1938), in an important series of papers published posthumously, found, by comparing the same adult organs in the complicated reproductive apparatus of thirty species of pulmonates, all transitional conditions from ordinary filamentous mitochondria to dictyosomes closely similar to those described in male germ cells. Moreover, in those species whose cells contain characteristic dictyosomes, during embryological development, the mitochondrial granules swell, then burst, to form the scales or dictyosomes, a name coined by Peroncito for the bodies in male germ cells, but used by many cytologists for similar bodies wherever found. This same process was even observed, in some species, during secretory cycles in adult animals. Ito (1941) found osmic-impregnated Golgi bodies in human spermatogonia in exactly that region of the cell where mitochondria could be demonstrated by other methods. All these observations argue against the universal acceptance of the identity of all types of Golgi apparatus.

Indirect proof that the form of the Golgi apparatus seen in fixed tissues exists in the living cell is deduced by Kirkman and Severinghaus (1938) from the fact that the Golgi apparatus behaves characteristically under varying physiological conditions and that it can be centrifuged and segregated from other cytoplasmic constituents. Is it quibbling to suggest that possibly fat droplets or vacuolar constituents or specially constituted regions of cytoplasm, perhaps rich in diffuse lipoids or such other substances as vitamin C, any of which might be responsible for the configurations resulting after impregnation, might vary in position during metabolism or during the application of high centrifugal force? Without asserting this to be the case, it seems to the writer that such "indirect proof" as that advanced by Kirkman and Severinghaus and others proves no more than the original impregnations.

Although Ludford in 1935 published a photomicrograph of such an apparatus in a living fibroblast cell which simply showed an irregular zone of clear cytoplasm not filled by bright granules or mitochondrial granules or vesicles, he stated as late as 1942 that it becomes visible only in degenerating cells or in cells stained with methylene blue. In his own words: "Under no other condition has any structure resembling the Golgi apparatus been seen in living cells in tissue cultures." It is, however, visible in both normal and malignant cells in culture media, after impregnation,

according to the same author. This would seem to indicate that the normal protoplasm must be altered, either by degeneration or by staining, before the apparatus can be detected. Warren Lewis has never seen anything resembling a classic Golgi apparatus in a living tissue culture cell (personal communication, 1944).

With regard to artefacts in cytology, Salazar (1942) says, "Demander une 'réalité essentielle' c'est faire une demande prehistorique" because everything one sees is artefact in the sense of metaphysical invariants.

PERMANENCE

Since all must agree that there is some basic reason, or reasons, for the invariable blackening with osmic acid or silver nitrate of certain parts of cells, the other questions enumerated in the Introduction become pertinent. As to the permanence of the apparatus, there is little new evidence to offer from the current literature. In the summary by Kirkman and Severinghaus, numerous authors are quoted who believe it to be a permanent cell structure as well as a few who suggest an origin de novo from nucleus or mitochondria or from the cytoplasm, but they leave the question open, pending further studies on early embryological development. They dismissed the observations of Parat regarding the origin of the Golgi apparatus in various embryonic cells with the statement that he followed the vacuome and not the Golgi apparatus through from egg to germ layer stages; yet it must be remembered that he used the same impregnation techniques that all cytologists use for the demonstration of this apparatus, and that no other Golgi apparatus was in evidence in the stages described. Worley and Worley (1943) traced vesicles which they called Golgi bodies from the mollusc egg into the veliger larva. The Golgi bodies described by them are identified by an unusual method. While these as well as the mitochondria may be stained with acid fuchsin, crystal violet, or iron hematoxylin in fixed preparations, those bodies which appear navy blue after methylene blue vital staining are called Golgi bodies whereas those that are pale blue-green are mitochondria. Worley (1944) found that in *Mytilus* they are also black after osmic acid. It may be remarked that Golgi bodies in general,—in gland cells, for instance—do not stain with acid fuchsin, crystal violet, or iron hematoxylin. However, the Golgi bodies, as identified by Worley, are observed to form fat or yolk or both, in the ovary, and in the embryo and larva as well. Since they continue to synthesize over and over, they appear to be permanent.

Gresson (1940b) observed that Golgi material was introduced into the egg of the mouse by the middle piece of the sperm, and from there it fragmented and was distributed throughout the cytoplasm of the fertilized egg.

Most observers have not been concerned with the first origins of the Golgi apparatus but have started with a well-formed structure and followed its continuity through various subsequent phases. Thus Andrew (1939) followed, in nerve cells of mice from 41 to 733 days old, a gradual fragmentation and final dispersion through the cytoplasm of bodies made visible by the DaFano method. They exhibited no cyclic changes with functional activity of the cells. Stein, Caldwell and Peters (1942) reported that in the anterior pituitary of the mouse there is a decrease in size of the Golgi apparatus, in all but the basophile cells, as the animal ages.

Hibbard (1942) observed changes during the development of the gizzard and proventriculus of the chick. d'Angelo and Charipper (1939) followed the Golgi apparatus of the thyroid during metamorphosis in *Rana pipiens* and observed an originally small compact mass at the apical pole of the nucleus growing into a more distinct network as the hind limb becomes 3 mm. long, becoming a compact mass of twisted rods when it is 18 mm. long, forming rings or nuclear caps when the fore limbs emerge, and forming greatly hypertrophied strands during tail resorption. In a more recent paper, d'Angelo (1941) attempted to correlate these findings with observations on the pituitary, but, while he concluded from changes in the cell types that the thyrotropic hormone is secreted by the basophiles, the pattern of the Golgi apparatus was not clear, and the conclusion was not based upon this structure. Wallraff (1939) followed the Golgi apparatus during the early development of the hypophysis in man.

The descriptions of germ cell changes during the passage of time, already numerous, include additions by Das (1939) on the oogenesis in Rhipcephalus, by Beams and Sheehan (1941) on human oogenesis, by Sluiter (1940) on that in the hen, and by Bhattacharya and Lal (1939) in a summary of oogenesis in general. Guthrie and Jeffers (1938), in a careful study of the ovary in two species of bats, report finding no Golgi apparatus as such, but only fat droplets that occupy the regions where

Golgi bodies are frequently described and which have the configuration of Golgi bodies. Papers by Sato (1940), Richter (1940), McCroan (1940), Mahoney (1940), Ito (1941), Chatton and Tuzet (1941), Rathnavathy (1941) and Gatenby and Collery (1943) describe the transformation of Golgi bodies during spermatogenesis in various animals.

Hirsch (1939a) thinks that the apparatus is permanent in some form in polyphasic secreting cells with recurring cycles, but that it may be lost from monophasic cells at the end of the single secretion synthesis. Since in the latter case the cell itself cannot work over again, the loss is immaterial.

FORM

As to the significance of the form of the Golgi apparatus, I quote from a review by Baker (1942). He speaks of the "casuistical arguments as to whether a given object—rendered visible by incomprehensible methods—is, or is not, to be regarded as a veritable Golgi body. No one knows what structure the ideal technique should show. The Golgi network is often spoken of but it may be queried whether this is often a good description. If such a thing could be constructed as a true model of the complex, magnified several thousand times, and if this model were shown to a member of the general public, it is possible that he would compare it to accumulations (or rows) of spheres embedded in a slimy looking material, or to spheres with bananas adjacent to them or touching their surfaces, or to spheres with separate strings intertwined among them, or even in some cases—if one may dare to suggest a heresy—simply to spheres; but the writer is doubtful whether the word network would often be used to describe the model, though it might occasionally be applicable." Simpson (1941) describes it simply as a twisted intra-cytoplasmic canal of uniform bore and filled with fluid. Bourne (1942) concludes that the apparatus is something which is constantly changing in form and therefore in fixed material presents whatever aspect it happened to have at the moment of fixation. And Salazar, to go back to 1936, wrote, "C'est comme la pluie qui tombe; elle forme un dessin de lignes qui rayent l'atmosphère, mais elle n'est qu'une série de gouttes qui se forment, puis tombent . . . ; l'appareil de Golgi des morphologistes c'est le schéma connu avec lequel des dessinateurs répresent la chose . . . "

While it has been stated that most of the work published during the first quarter century of study of this body was descriptive of its morphology alone, it must also be admitted that morphological aspects continue to play the major role in the more recent attempts to correlate the apparatus with physiological processes. The question as to the significance of its form continues to pose itself. Severinghaus was able to identify the acidophilic and basophilic cells in the hypophysis of the rat on the basis of the form of the Golgi apparatus alone. Poris (1941) also found the apparatus in reptiles to be more compact in acidophiles than in basophiles, though its location in the cytoplasm was variable. On the other hand Copeland (1943), in *Triturus*; Aplington (1942), in *Necturus*; Payne (1942), in the fowl; and Ayres (1941), in the immature rat, found no identifying differences in the Golgi apparatus of hypophysis cell types.

Several authors are so convinced of the validity of its morphology as to base functional interpretations on the observed forms. Thus Baillif (1941) uses the Golgi configuration as an indication of phagocytic response in the rat omentum; Welch and Brodus (1940) found it a delicate method of estimating cellular function in the human thyroid. They interpreted cases of adenomatous goitre, not diagnosed as hyperthyroids, as mild cases of hyperthyroidism notwithstanding the diagnosis, solely because some of them had the marked hypertrophy of the Golgi apparatus found characteristically in exophthalmic goitre. Dalton and Edwards (1942a) found it to be of value in diagnosing mouse neoplasms; but Rauramo and Turpeinen (1940) found a Golgi apparatus in only about half of the seventeen uterine carcinomas studied. Krichesky and Mandel (1943) made careful measurements of cell size and the size of the Golgi apparatus in the uterine glands of the rabbit during pregnancy, and concluded from their results that our ideas of the function of the uterine secretion should be modified. Before the free blastodiscs become implanted the secretion is assumed to act as a nutritive agent, and when the uterine muscles are contracting vigorously the secretion could provide lubrication, but since they found little correlation between the dispersion of the Golgi apparatus and the occasions when an increased secretion would be useful, Krichesky and Mandel conclude that the secretion is not increased at these times and therefore cannot have the functions ascribed to it. They suggest no doubt of the validity of using the morphology of the Golgi apparatus as a measure of secretory activity. Seshacher (1942) used the Golgi apparatus to identify oocytes developing from primor-

dial germ cells in male Apoda and distinguish them from primitive spermatogonia.

In view of the large number of papers by Hirsch and his co-workers, including the Protoplasma Monograph (1939a), which have appeared since the summary by Kirkman and Severinghaus, the morphological data the former have accumulated and their interpretations of it must be discussed. They have examined many types of cells directly, and Hirsch has gone further and re-interpreted the observations of other cytologists in terms of a basic pattern which fits all cases. According to this pattern, there is in each cell a primordial "presubstance" which is homogeneous, though not necessarily a single chemical compound. It often stains with neutral red, usually blackens with silver nitrate and osmic acid. Its origin is shrouded in mystery, awaiting proof as to whether it arises from the cytoplasm directly, or the nucleus, or the mitochondria, or from an interaction of some or all of these. It may appear in the form of droplets, a beaded string, an irregular mass (possibly only when over-impregnated, so as to conceal its true form), elongated threads, or a network. During cellular differentiation or cellular functioning this primordial presubstance develops into the "Golgi system," which is a duplex affair composed of osmiophilic and osmiophobic parts, or Golgi-externum and Golgi-internum. The internum is what Salazar calls the "para-Golgi apparatus." (See 1942 and earlier papers.) In the production of the internum, the cytoplasm with its mitochondria undoubtedly plays some part, though it is not demonstrable morphologically in most cases. Hirsch lists twenty-five cases of vertebrate cells and twenty-one among invertebrates which exhibit this duplex character. Turner (1940) found duplex bodies in Protozoa; Filhol (1938), in his pulmonate material, was always able to see a duplex composition in the impregnated tissues; Dornesco (1938) concluded from extremely careful studies that, in the rat and guinea pig nerve cells, the networks often described were the result of seeing overlapping but discrete dictyosomes. The Golgi-internum, according to the Hirsch school, is the site of the synthesis of the cell's product, secretory granules or yolk, for example. Jacobs believes that the internum increases at the expense of the externum, but Hirsch prefers to think of the externum as gathering and transporting materials from the cytoplasm to the internum. When the synthesis is complete, the product is rolled out of the system into the cytoplasm, and the "Golgi-remnant" remaining behind becomes new presubstance to repeat the cycle in polyphasic cells. The apparently missing osmiophobic component in vertebrate somatic cells, Hirsch thinks is to be found in the granule or vacuole that develops inside the net and that has been frequently overlooked by observers or ruled out of the Golgi picture as a case of Parat's "vacuome" and thus not a part of the apparatus. The network itself, except for a possible net of presubstance, Hirsch thinks is often an artefact of over-impregnation, since each internum has its own externum. Where many of these are aggregated within a small space they may overlap and appear continuous. There may be, however, in addition to the mono-systems, true poly-sys-

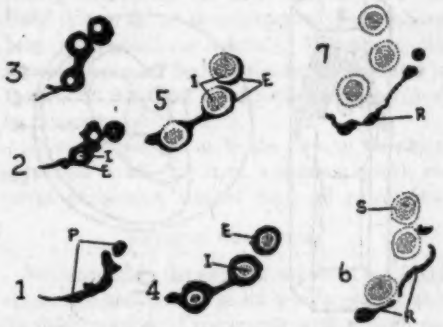

FIG. 3. HALF SCHEMATIC DIAGRAM OF THE SECRETION CYCLE OF THE GOLGI APPARATUS IN THE PANCREAS OR SALIVARY GLAND

E—externum; I—internum; P—presubstance; R—Golgi remnant; S—product (after Hirsch, 1940a)

tems in which the externum may remain continuous around a group of internums. The recent studies by Worley and Worley (1943) and Worley (1943a, b, 1944a, b) seem to fit the Hirsch pattern almost exactly. The following diagram taken from Hirsch (1940a) summarizes these concepts.

In the same year that Hirsch's monograph appeared, a careful study of many amphibian tissues was made by Pollister (1939), in which the form of the Golgi apparatus was demonstrated, after careful measurements, often using all of the serial sections of a single cell, to consist of a plate-work of irregular shape but always of uniform thickness, about 0.2 of a micron. This study was purely morphological and based entirely on impregnated sections. Pollister's conclusions can best be illustrated by two schematized drawings from his paper, indicating his suggested classification of all cells

into those that are polarized and those that are non-polarized, from the physiological angle. In this connection, Pollister classifies the cells of the adrenal medulla, embryologically related to nervous tissue, as the B or physiologically unpolarized type. Bennett (1941) has shown that in the cat these cells have a strict orientation, with one pole toward the venous capillary and the other toward an arterially supplied capillary. The secretion is toward the venous capillary, and nerves may be demonstrated in contact with the opposite end. The Golgi apparatus is polarized toward the vein.

As Pollister (1939) reminds us, the general arrangement of the Golgi apparatus among invertebrates seems to be that of a widely scattered dis-

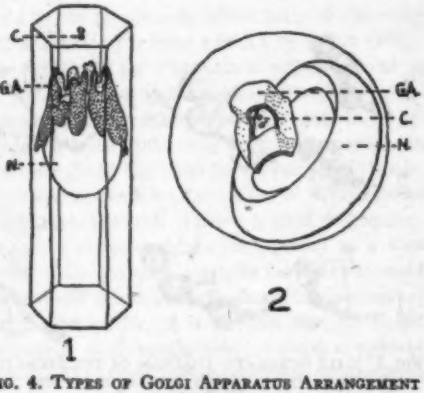

FIG. 4. TYPES OF GOLGI APPARATUS ARRANGEMENT IN AMPHIBIA

1. The epithelial or polarized type. 2. The leucocyte or unpolarized type. C—centrioles; G.A.—Golgi apparatus; N—nucleus (after Pollister, 1939).

tribution of discrete elements; that in the somatic cells of vertebrates is more often a compact polarized affair, whether it be made of separate units or fused into a net or plate-work or canal. Some recent studies do not fit this general pattern, as, for instance, Subramaniam (1939a), who found that in *Branchiostoma* the apparatus is unpolarized and not as usually found in the vertebrates; Sosa and Menegazzi (1940), who found networks in leech muscle; Dehorne (1938), who found it to be polarized in Nereis, and (1939b) unpolarized in the toad pancreas; James (1939), who reported in eosinophiles of the *Necturus* thymus a dispersed perinuclear Golgi apparatus, partly branching and partly in the form of isolated rings; and Filhol (1938), who found polarization in the pulmonates. Filhol developed an interesting theory that the pulmonates exhibit a kind of transitional stage between the two types of distribution since, though invertebrates, they usually have a Golgi zone but no network. In another paper Feyel and Verangot (1938) recall conclusions previously reached by the first author that excretory cells of invertebrates have a purely vacuolar Golgi apparatus (discrete elements), but that the higher we go in the animal series, the more complex it becomes.

The position of the Golgi apparatus has been studied for the most part in mononuclear cells, but the situation in multinuclear cells, where the nucleocytoplasmic interchanges or forces might be expected to differ from those in mononuclear cells, has been described by several recent observers. Rossman (1940) has found in deciduomata of monkeys the Golgi apparatus in multinuclear cells to be dispersed or to exhibit some anastomoses, but there is never any polarization with respect to the nuclei. In human lympho-ganglionic tissue in Hodgkin's disease, Buno (1938) found only one Golgi zone, no matter how many nuclei. It occupied the central space between the nuclei, if such a space existed. Watzka (1939) frequently found, in binucleate cells in rabbit sympathetic ganglia, a separate Golgi zone associated with each nucleus. Thus, at present, no common feature emerges as to the Golgi body's relation to the nuclei.

There have been several passing references to vacuoles and the vacuome hypothesis already in this paper, and no discussion of the form of the Golgi apparatus should fail to take account of the fact that vacuolar spaces or their walls frequently are blackened after osmic acid or silver nitrate impregnation. Kirkman and Severinghaus treat the matter as of historical interest only and claim that the whole idea that these structures might be Golgi apparatus has been completely disproved. Without evaluating the various researches which they marshall in support of this idea (p. 569), it may be said that other more recent publications, including those of Mahoney (1940), Clement (1938) and Champy and Coujard (1939), add a further weight of numbers to their list. There is, however, something to be said on the other side of the question. Cowdry (1938) has found no reason to depart from the idea of the relation of neutral red vacuoles to certain of the blackened nets in impregnated material, a relation such as he and Scott described in 1928, as occurring in the malarial parasite, where neutral red granules fuse to form an osmic impregnated Golgi net. Feyel and Verangot (1938) observed, in the normal human

thyroid and in exophthalmic goitre, the vacuome (not to be confused with Bensley's vacuoles),—frankly so-called, although it was demonstrated by impregnation with silver nitrate and corresponded to what others have called the Golgi apparatus. They found that a concentration of the vacuome in a local region is characteristic of a stable metabolism, whereas a spreading of the vacuoles throughout the cytoplasm occurs during hyperactivity of the cell. In the latter case there is no Golgi zone. Filhol and Garrault (1938) found in the Golgi zone, in four species of selachians, only a vacuome-chondriome complex. Feyel (1939) interpreted all silver nitrate blackened bodies in the guinea pig hypophysis as vacuoles with mitochondria on their surfaces. Järvi (1939), working on the sublingual glands of the cat, figured a strikingly vacuolated Golgi apparatus, present especially in the protein cells and in the mucus cells, an hour after pilocarpine injection. Vetter (1940), by injecting trypan blue into mother mice and rats until their milk was blue, was able to observe blue vacuoles in the Golgi zone in the intestinal epithelium of the suckling babies. Hibbard (1942) saw neutral red vacuoles in the digestive tracts of chick embryos and young chicks, corresponding in every stage, even in cases of reversed polarity, to the position of the Golgi apparatus, although, since the impregnated apparatus was not visible in live cells, there was no proof as to whether the vacuples were between the strands of the Golgi apparatus, or within them, or forerunners of them. Contrary to statements frequently appearing that Parat simply thought that the vacuoles were in reality the Golgi apparatus, because of their capacity for impregnation, that was but one aspect of his complete concept. Stated in brief, he found that so many different things could be impregnated that it would be better to distinguish each of them by their individual names rather than lump them in one category. He differentiated: vacuoles, either separated or flowing together during fixation and impregnation; mitochondria, either ordinary chondriosomes or hypertrophied ones—he thought the dictyosomes of male germ cells and certain larger chondriosomes in special glands were of this type; diffuse cytoplasmic lipoids attracted to the interfaces of vacuoles or chondriosomes and the cytoplasm; or any combination of these. Recognizing the inter-relations between many of these cytoplasmic inclusions, Baker (1944) attempts to resolve the confusion by using the overall name "Golgi element" to include four parts: the vacuoles stainable by neutral red, the dense lipoid-containing substance (osmiophilic and stained by Sudan black), the Golgi product (secretion granule) and the diffuse lipoid-containing ground substance which fills in all the rest of the space in what others have called the Golgi zone. Parat noted, as many subsequent observers have done, that additional vacuoles were formed by the action of neutral red, and this fact has led some observers to conclude that all neutral red staining vacuoles are abnormal to the living cell, but there seems to be ample evidence that there is a normal vacuome existing in cells before the provocation of additional vacuoles by foreign agents. Worley (1943b) states, "It appears very probable that there is a correspondence between the 'vacuome' and the Golgi system in far more instances than we have been accustomed to believe." Related to the idea of a vacuolar form of the Golgi apparatus is the concept that it is a canal, such as that described by Simpson.

Thus the question as to the form of the Golgi apparatus is still far from a solution which receives unanimous support from all cytologists.

PHYSICAL CHARACTER

With regard to the physical nature of the Golgi apparatus, questions as to its specific gravity and its fluidity arise. Experiments with centrifugation throw light upon this subject. In earlier summaries the conclusion has been reached that the Golgi apparatus is lighter than the cytoplasm. It usually lies centripetal to the mitochondria, but Beams and King (1938), in 25 per cent of the guinea pig eggs centrufuged by them, found the yolk nucleus (Golgi apparatus) among the mitochondria at the heavy pole, and in the other 75 per cent it was nearer the middle but heavier than yolk, clear cytoplasm, and fat. Gresson (1940a), examining the mouse oocyte, found these bodies near the middle. Richter (1940) could not determine, in the spermatocytes of *Notonecta*, which was the centrifugal pole, but at some stages the idiosome spheres were not attached to their Golgi caps, and in such cases the two portions of the apparatus moved to opposite poles. The idiosome-Golgi cap complex, or the Golgi cap in the dissociated phase, moved to the same pole with the mitochondria. This seems to be another similarity of the male germ cell dictyosome with mitochondria (see p. 4).

As to the fluidity of the Golgi apparatus, it has

been described both as very fluid and as relatively solid. New work adds evidence to both sides of the question. Pollister (1939) assumed that the Golgi apparatus cannot be fluid, nor even a highly plastic solid, and at the same time maintain its platelike form, though he found it elastic to the extent that bending due to pressure from the gastric contents is straightened again when the pressure is removed. At the opposite extreme are the views of Simpson (1941), who assumes it to be of the greatest fluidity because of its distortion upon freezing (see p. 11); and of Worley (1943b), who observed vesicular Golgi bodies readily collapsing and discharging their fluid contents into the cytoplasm when treated with hypertonic salt solutions.

CHEMICAL COMPOSITION

The widely accepted idea as to the chemical constitution of the Golgi apparatus is that it is lipoidal

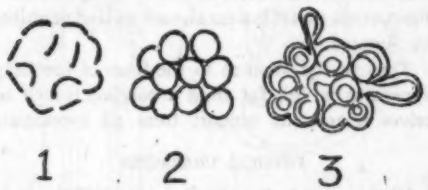

FIG. 5. THE EFFECT OF SODIUM BICARBONATE ON THE GOLGI BODIES IN HELIX SPERMATOCYTES

1. Golgi bodies in the normal state. 2. Golgi bodies assuming globular form in sodium bicarbonate. 3. Myelin figures growing out of Golgi bodies after a longer treatment with sodium bicarbonate (after Monné, 1939b).

or lipo-proteic. MacLennan (1943) classified the intermediate lipoid bodies in the Protozoa among the Golgi bodies on the basis of the general acceptance of the lipoid constitution of the latter wherever found. Ever since the statement made by Sjövall in 1906 that the Golgi apparatus was lipoidal in nature, a statement not based on anything like modern histochemical tests, the literature has been full of tacit assumptions that it is lipoidal. Monné (1939b), using Helix spermatocytes observed under dark field illumination, found that by adding sodium bicarbonate solution, the dictyosomes (which he assumed to be the Golgi apparatus) became lighter in color, then swelled and showed a tendency to coalesce, and finally gave rise to typical myelin figures. His explanation for this behavior was that the lipoids in the shell of the Golgi apparatus gave rise to the myelin figures. (See fig. 5.) Baker (1944) proved by a variety of additional tests that these bodies in *Helix* probably contain lecithin or cephalin or both. The conspicuous dictyosomes that are found in spermatocytes clearly have lipoidal constituents, but that this is true of the more elusive apparatus of somatic cells is not so clear. There is a good deal of evidence that the germ cell dictyosomes are not the same thing as the blackened apparatus in many somatic cells (see p. 4), and if these are different categories of inclusions, the generalized statement that all Golgi bodies are lipoidal is unjustified.

MacLennan has stated that both lipoidal and non-lipoidal bodies in the Protozoa react identically to Golgi techniques. This author included among these, fatty acid bodies or intermediate lipoid bodies, granules and membranes associated with the contractile vacuole, and granules with a secretory cycle which are neither lipoidal nor excretory. However, he referred to the fatty acid bodies or intermediate lipoid bodies as Golgi bodies. Meglitsch (1940), on the other hand, considered the secretory granules to be the Golgi bodies, and found that they stain with neutral red. Still other workers identify the osmiophilic cortex of the contractile vacuole as the Golgi apparatus,—for example, Gatenby and Smyth (1940), who described its behavior in rapidly dividing and in non-dividing cultures of *Copromonas*. Smyth (1944) sums up the various Protozoan structures that have been described under the name of Golgi apparatus.

Much of the experimental work in centrifuging the apparatus to the lighter pole of the cell in Metazoa has been used to furnish proof of its lipoidal constitution. Bourne (1942), after stating that Golgi bodies are soluble in fat solvents and therefore contain a high percentage of fats, and mentioning their reduction of osmic acid and the centrifuging experiments, concludes that they are probably fatty and protein, with the latter on the outside, so that they cannot be stained with fat dyes. Watzka (1939) found that the Golgi apparatus breaks up and disintegrates after chloroform narcosis, suggesting that it has a lipoidal character. Hirsch thinks the presubstance blackens because of unsaturated fatty acids contained in it. He believes it must be a chemical mixture, possibly a different mixture in different cells, although it appears structureless; but this needs to be proved. Salazar (1943a) states that the Golgi apparatus may possibly be lipoidal or lipo-proteic but the the para-Golgi apparatus inside it is never lipoidal. Worley (1943a) assumes the Golgi body in mol-

luscs to be a more or less spherical vesicle with a chromophilic, gel-like, relatively lipoidal pellicle covering a relatively more protein, fluid, chromophobic core.

Perhaps the most painstaking work on the chemistry of the apparatus is the work by Simpson (1941), and since Kirkman and Severinghaus expressed a hope that the method he used, the freezing-drying method, might throw much light on this aspect of the subject, a more extended review of Simpson's paper will be made. Since the cells (from epididymis, duodenum, and pancreas of the guinea pig, and spinal ganglion of the rabbit) were to be examined cytologically after the freezing-drying technique, careful controls were studied at each stage of the freezing and drying to determine where any artefacts due to freezing might be found. At slow speeds of freezing and even at certain zones parallel with the surface when freezing was very rapid, at −195°, there were damaged regions due to ice-crystal formation, but in the well-preserved areas, Simpson asserts that the fixation and preservation were superior in excellence to that in the best chemically fixed sections. The form of the apparatus proved in all cases to be a coiled canal, of uniform bore, within the cytoplasm. Examination of the frozen-dried Golgi apparatus by means of dark field illumination or with the polariscope showed no optical distinction from the surrounding cytoplasm. The contents of this canal could not be impregnated with osmic acid, nor even its surface, in pieces which were completely dried. In frozen bits of tissue which were allowed to thaw in Golgi fixatives and then impregnated, some blackening occurred, though it was not as clear as after the ordinary methods without freezing. It was usually the outside and not the contents of the canal which blackened. It appears that there is no lipoid or specific osmiophilic substance in the Golgi apparatus, unless it was altered by the freezing and drying. The apparatus was not readily stainable as thus prepared, but was clearly visible when the rest of the cell was stained. To test its possibly scanty lipoidal contents, tissues after freezing and drying were subjected to boiling absolute alcohol for 24 hours and subsequently to boiling anhydrous chloroform for another 24 hours, after which its stainability was found to be enhanced. Fine fibrils could be demonstrated inside the tubule, which stained with resorcin-fuchsin, from which fact Simpson concludes that the Golgi apparatus contains very diffuse proteins that were not stainable in the first instance because the protein molecules were too dispersed by faint traces of lipoidal material. When the vigorous fat extraction had been accomplished, the protein molecules were allowed to aggregate into the fine fibrils, which were stained as elastic fibers are stained by resorcin-fuchsin. (Weigl in 1910 was able to stain with this dye after bleaching an osmic impregnated nerve cell.) Injections of neutral red into animals before killing produced *de novo* droplets in the epididymis cells distal to the nucleus, in the area where the secretion granules were forming but distinct from the Golgi canal. While the Golgi apparatus after freezing and drying failed to show any impregnation with osmic acid, there were produced finely dispersed black granules throughout the cell. The point is not emphasized by Simpson but there is the possibility that a dispersed material or materials might accumulate during special chemical fixation in the fluid canal to give it the osmiophilic quality generally observed. Simpson indicates the high fluidity of the apparatus in the cells he studied, by pointing out that it is highly susceptible to "blowing up" on freezing in the imperfect zones of the block.

Vitamin A is apparently not associated with the Golgi apparatus. Since Popper (1944) has found it, in the liver and adrenal gland, practically always bound to intracellular lipids demonstrable by sensitive stains, its absence on or in the Golgi apparatus might be taken as additional evidence of the absence or very high degree of dispersion of lipoidal constituents in that apparatus.

Professor R. R. Bensley, who has done me the honor of reading this manuscript, is inclined to think of the Golgi apparatus, exclusive of that in spermatocytes, as a system of vacuoles or canals containing very highly dispersed lipoidal, protein, and other organic and inorganic constituents more or less specific for the type of cell containing it, and dependent, within limits, on the permeability of its surface membrane and the metabolism of the type of cell concerned. (Personal communication, 1944.) This suggested specificity of chemical composition to the type of cell is illustrated by Emmel (1945), who found alkaline phosphatase in abundance in the Golgi apparatus of the absorbing cells in the intestine but not in that of the absorbing cells of the proximal renal tubule.

FUNCTION

There is perhaps more agreement among cytologists that the Golgi apparatus is secretory in func-

tion than about any other aspect of the problem. And yet even here the questions as to whether it is transformed directly into the secretion product (as is the internum of the apparatus according to Hirsch, *et al.*), or whether the apparatus is instrumental in forming the secretion outside itself (Järvi, 1940), or whether it is only indirectly concerned, as shown by enlargement of the apparatus during the formation of the secretion products though it may not be in direct contact with the secretion (Aplington, 1942; Copeland, 1943; Deane, 1944a, b; Goormatigh, 1940). In the pancreas of the cat and mouse, Järvi (1939) found no great variation in the size of the Golgi net, but the secretion granules arise in its meshes. But there were reported no activities of the apparatus correlated with secretory cycles in most of the cells of the *Triturus* hypophysis (Copeland, 1943), in the hypophysis of the fowl (Payne, 1942), in the salivary glands of twenty species of Hemiptera (Baptist, 1941), in the adrenal of the cat (Bennett, 1940, 1941), or in neurosecretory cells in fish (Palay, 1943a). Reese and Moon (1938) reported some hypertrophy of the Golgi apparatus in the fascicular zone of the adrenal cortex after adrenocorticotropic hormone injection. Ponse (1938) found no hypertrophy, fragmentation, or disappearance of the Golgi apparatus in the thyroid, but she found some relation to the secretory pole of the cell, since in normal glands only one cell in 500 showed reversed polarity, while in glands activated by thyrotropic hormone one cell in 10 showed reversed polarity. Among the many publications adding evidence to the idea of the secretory activity of the Golgi apparatus are those by Hirsch and his associates (Järvi, Breitschneider, Jacobs, von Weel, Sluiter, Rinkel, *et al.*); in fact, their contribution is largely based on tracing the process of secretion formation by this structure in many types of cells. Also Subramaniam (1938b) found Golgi crescents adhering to watery and granular secretions, and from their shape and position assumed they secreted the enzymes in Lumbriconereis intestine cells. Aykroyd and Gatenby (1941) found in human uterine glands definite changes of the Golgi apparatus correlated with functional activity. Foster (1943) concluded that varying structure in cells of the parathyroid corresponds to functional cycles. Ayers (1941) observed vesicles moving out from the Golgi net in the young rat hypophysis and suggested the origin of the endocrine secretion by this means. Worley and Worley (1943) and Worley (1944a, b) described the synthesis of protein and fat both in and on the Golgi apparatus of mollusc embryos and larvae. Worley (1943a) finds its ability to absorb and to segregate materials from the cytoplasm to be its two most fundamental physiological characteristics. Miller and Riddle (1942) thought that the Golgi net was not instrumental in the formation of lipoid granules in the pigeon adrenal cortex, but since the net expands later into fine strands between these granules it may play a part in transforming the precursor substance into the true hormone.

It is in connection with its secretory function that there is the greatest volume of evidence for the homology of the Golgi apparatus of germ cells with that of other cells, outside of its impregnation with osmic acid and silver nitrate. Worley (1939) compared the sperm-forming cells in decapods having nonflagellated spermatozoa with cells giving rise to the more usual flagellated spermatozoa, and assumed homologies in the completed cells based on similar transformations or secretions of duplex dictyosomes or Golgi bodies. So widespread is the idea that the Golgi apparatus is concerned with secretory phenomena that Dalton and Edwards (1942a, b) finding in hepatic tumors of rats and mice that the Golgi material remained invariable, as a condensed juxta-nuclear net, concluded from this that there was an absence of exocrine secretion. Dawson (1942) summarizes, "It is clear that no final disposition of the problem of the role of the Golgi apparatus in secretion can be made until cytologists decide whether the Golgi apparatus is a single entity of specific composition or a complex of several systems closely associated topographically, and perhaps functionally, within the cell."

There is some evidence, too, that the Golgi apparatus is concerned not only with secretion but with absorption (van Weel, 1938a, b, 1939; and Vetter, 1940). Pfuhl (1938) and Pfuhl and Dienstbach (1938) found that injected colloidal dyes and Chinese ink were absorbed by the liver cells into the Golgi apparatus.

An extraordinarily interesting aspect of the question has come to light in studies which localize vitamin C (ascorbic acid). Bourne (1942) thinks the vitamin goes inside the Golgi apparatus and there, protected from reactions in the general cytoplasm, it takes part in the synthesis of secretion products. Its position in the Golgi apparatus may also aid in the passage of substances across the placenta or the kidney tubule by protecting the

diffusing substances from the powerful reducing action of the vitamin. Fischer (1938) observed changes in the polarity of the Golgi apparatus during diuresis.

Many substances have been reported to be adsorbed on the Golgi apparatus, including iron (Hirsch), lithium carmine and trypan blue (Fischer, 1938), various other metals (Van Tiel, 1940), benzpyrene (Graffi, 1940) and among them, vitamin C. Hirsch, however, suggests that the vitamin is not adsorbed by the apparatus but condensed by it. Among recent workers who showed the location of the vitamin to be in the Golgi apparatus may be cited Järvi (1940b), Faller (1941), and Tonutti (1940), who in addition figured its active emission from the apparatus in the functioning adrenal cell.

Barnett and Bourne (1941) found, in the early development of the chick, that during the first eighteen hours the vitamin was localized only in the peripheral cells of the blastoderm in contact with yolk granules. (Parat found the first "Golgi apparatus" in several invertebrate embryos in contact with yolk granules.) From the first to the third day it is in the extra-embryonic membranes only, but beginning with the fourth day, it is found in the cells of the embryo itself (central nervous system, liver, pancreas, myotome, etc.). They conclude that quantities of the vitamin in the reduced state are not necessary for the initial rapid growth; that while it is probably utilized by these early tissues (some blackening of blood vessel walls, coelomic cavity, and neural tube walls in the first three days may indicate its passage into the tissues), the oxidation potential in the young cells is so high that the vitamin is oxidized immediately on reaching the cells. It is well known that studies on the Golgi apparatus in these same earliest embryonic cells are rare, though many descriptions exist for later stages of embryology. Possibly the cellular differentiations at these early stages have not yet reached a point where a specialized protective region of the cytoplasm can conserve the reduced vitamin. However, Weed (1937) described a Golgi apparatus in the primitive muscle cells of a 40-hour chick embryo.

Barnett and Bourne (1941) also studied the later development of the chick embryo and concluded that the reduced silver deposits (vitamin C) in the liver, kidney, ovary, and nervous system were actually in the Golgi apparatus. They found no support for the view that the vitamin may be on or in the chondriosomes. They could find no deposits in cells of the testis. The account of Kehl (1939) presents the earliest picture of Golgi apparatus in the chick testis, and the primordial germ cells were there distinguished from the vegetative cells destined to form Sertoli cells by means of the orientation of the Golgi apparatus. This work, however, was done on chicks two to three days after hatching, while Barnett and Bourne studied embryos. Faller (1941) studied the vitamin C distribution in the testis of the rat but was apparently concerned only with the vegetative cells. It would be extremely interesting to know whether a difference in vitamin C content might be added to the numerous other differences between male germ cell dictyosomes and the Golgi apparatus of somatic cells.

Barnett (1942) found vitamin C in the Golgi material or on fat droplets in cultured heart, bone, and adrenal cells, but only in a few cells. Those with the greatest amount were degenerating cells. It will be remembered that Ludford stated that only in degenerating cells in tissue cultures could the Golgi apparatus be seen while the cells were alive and unstained. Barnett and Fisher (1943) further point out that, as in the deposition of osmic acid analysed by Bensley and Owen, the position of the precipitate on the Golgi substance does not prove that the vitamin was in that position in the functioning cell; the vitamin was somewhere in the cell, and the silver which is reduced by it may simply settle at an interface provided by two immiscible materials.

Since so much doubt has been cast on the reliability of impregnation methods for the demonstration of the Golgi apparatus, some consideration of the methods for the demonstration of the vitamin histologically are pertinent. While the Cajal and DaFano methods for Golgi apparatus depend on special fixation and subsequent reduction of the silver salt, the vitamin C reaction depends on direct reduction (see Giroud, 1938; Barnett and Bourne, 1941). The resulting blackening parallels the results obtained by the chemical method of titration with dichlorophenolindophenol and also the biological findings on the antiscorbutic action of the vitamin. In those animals which are unable to synthesize Vitamin C, and which are subjected to a scorbutic diet, the cellular granules progressively disappear. Reduced silver granules are not produced by other cellular reducing agents; removal of lipoids from the cell by chloroform does not change the reaction, though aqueous solutions may wash out the vitamin.

TECHNIQUES OF INVESTIGATION

Recognizing the sorry state of affairs existing because of conflicting interpretations based upon the only diagnostic methods of demonstrating the Golgi apparatus, by means of impregnations, many investigators have attempted to find out what we are dealing with by other means, always returning to impregnations to be sure they were correctly identifying it. Thus, as has already been mentioned, displacing the Golgi apparatus by means of centrifuging and the freezing-drying technique have been tried. Parat's followers still use "techniques convergantes," by which they mean that all types of fixatives and stains, including histochemical tests and vital examination are focussed on a given cell. The "Stufenuntersuchungsmethode" is used by Sluiter and others in Hirsch's school, meaning a study of the cell through all its functional phases.

The physiological state of cells has been experimentally altered by feeding (van Weel, 1938a, 1939); or by hormone action (Ponse, 1938; Reese and Moon, 1938; Miller and Riddle, 1942; *et al.*); or by starvation (De Robertis, 1939); or by temperature variations (Radsma and van Weel, 1940, who raised rats from a tropical environment in cool surroundings and found their thyroid Golgi apparatus disappeared in thirty days, not to reappear as a normal reticulum until the third generation); or by varying the water balance (Fischer, 1938; Emmel, 1938); or by forcing a muscle cell to work. Roskin (1938) found no change in the Golgi apparatus of the smooth muscle of Amphibia after five hours of working in vitro; but Sosa and Menegazzi (1940) were able to demonstrate changes in structure with contractile activity in the leech muscle. Waugh (1942) found that various sulphonamides affect the Golgi apparatus in the chick embryo, causing fragmentation. Dooley (1941) found the dictyosomes of male germ cells of Orthoptera to be peculiarly resistant to changes resulting from high concentrations of colchicine which altered all other cytoplasmic inclusions.

Different methods of observation have been used by Monné (1939a), who used the dark field illumination on *Helix* spermatocytes already described. Viewing them by means of polarized light, Monné (1939b) also found that the outer part of the Golgi bodies in these pulmonate spermatocytes is birefringent, though he cautions that the light must be of the strongest possible intensity, and that though visible unstained, they are much more brilliant when vitally stained with chrysoidin. The Golgi elements are lens-shaped with an outer layer which he concluded contains lipoid molecules perpendicular to the surface. It will be recalled that Simpson found no optical differences by using Monné's methods of illumination.

Tarao (1940) found that after over-night digestion in trypsin of formol fixed sections of mouse pancreas, it was possible to stain the Golgi apparatus with Nile blue sulphate. Worley and Worley (1943) used vital staining with methylene blue to demonstrate it.

CONCLUSION

So we are back at the point where we started. In the face of the statements by Kirkman and Severinghaus (p. 558) that "The literature records instance after instance in which intracellular vacuoles or canals, preformed or induced, prozymogen granules, intracellular lipoids, deposits of osmium on Nissl bodies and mitochondria have been mistaken for Golgi material" (bibliographical references omitted), and farther on, that "it seems likely that mistaking the identity of the Golgi apparatus in most vertebrate cells at least, is largely a thing of the past," examination of current literature nevertheless reveals vesicles or vacuoles (Worley), intracellular canal (Simpson), prozymogen granules (Hirsch), intracellular lipoids (MacLennan, and Guthrie and Jeffers), and modified mitochondria (Filhol, Feyel, and Dehorne), all identified as Golgi apparatus. Progress cannot be made by confusing unlike structures.

In conclusion, the Golgi apparatus might still be defined as that cytoplasmic structure or structures which blacken with osmic acid or silver nitrate and which, in the opinion of the observer, is not something else. The lack of unanimity on every aspect of the subject strongly suggests that cytologists are not all studying the same thing, in spite of the fact that they all use the same name for it. This review of recent findings proves that more than one category of inclusion is still being blackened and described under the name "Golgi apparatus," and that efforts to generalize by assuming that the behavior, structure, and physicochemical composition observed in any one case are applicable to the "Golgi apparatus" in the abstract sense cannot but result in contradictions. With regard to most of the generalizations, we should be better off if the discovery of the impregnation methods had never been made.

There are, however, some bright spots. To quote Okkels (1934), "It is true that the classical Golgi apparatus is more or less an artefact. But

it is a regular one, claiming as such scientific importance." Artefact or not [Tarao (1940): "The Golgi apparatus . . . is too beautiful to be an artefact"], when it varies regularly with functional states in a given cell, it indicates something, even though we do not know what, about the activity of that cell. Its diagnostic value has been mentioned. And the dictyosomes of male germ cells are certainly not artefacts. Though it seems unlikely that they are the same as other structures bearing the name Golgi apparatus, observations of their peculiar behavior during spermiogenesis have added to our knowledge of that process.

The decrease in the number of papers dealing with what is still a much misunderstood, as well as little understood, field of research appears to be due less to any general agreement among cytologists as to a solution of the problem involved, than to a disillusionment with regard to the methods employed to find those solutions. Since the methods of metallic impregnation bring forth only morphological features, and since even these methods are not specific, some other avenue of approach becomes necessary. Thus, Guthrie and Jeffers (1938), assuming that, in egg cells at least, "so-called Golgi bodies" are products of cellular metabolism, state: "We do not use this designation" (Golgi apparatus) "because of the vitalistic concepts that have become associated with it." D'Arcy Thompson (1942) points out "the inevitable fact that dynamical problems lie behind the morphological problems of the cell." This idea is surely in the minds of cytologists who go to so much trouble to describe the morphological aspects, as evidenced by Parat's reasoning that the vacuomechondriome complex as he saw it in spermatocytes and in gland cells was important as a means of separating yet keeping close together, different solvents in order to orient molecules for syntheses. Hirsch goes to some trouble to suggest the similarity of coacervates and the surfaces of the Golgi apparatus. But these and similar suggestions arise more from thinking about the apparatus than from direct observation of it. It may well be that until we can attack the whole problem of cellular functioning in a more minute manner, further discussions about the materials blackened by metallic impregnations are fruitless. Needham (1942) reminds us that "the chemical structure of molecules, the colloidal conditions in the cell and the morphological patterns so arising, are inextricably connected. . . . We are driven to the view that the living cell possesses as complex a set of interfaces, oriented catalysts, molecular chains, reaction vessels etc., as the organs, tissues and other anatomical structures of the whole organism." In these terms our present knowledge is in the most elementary, gross form.

LIST OF LITERATURE

(With few exceptions the literature citations are from 1938 on.)

ANDREW, WARREN. 1939. The Golgi apparatus in the nerve cells of the mouse from youth to senility. *Amer. J. Anat.*, 64: 351–375.

ANGELO, SAVINO D'. 1941. An analysis of the morphology of the pituitary and thyroid glands in amphibian metamorphosis. *Amer. J. Anat.*, 69: 407–437.

——, and HARRY A. CHARIPPER. 1939. The morphology of the thyroid gland in the metamorphosing *Rana pipiens*. *J. Morph.*, 64: 355–372.

APLINGTON, HENRY W., JR. 1942. Correlative cyclic changes in the hypophysis and gonads of *Necturus maculosus* Rafinesque. I. The male. *Amer. J. Anat.*, 70: 201–249.

AYERS, JOHN C. 1941. The Golgi material in the hypophyseal cells of the immature albino rat. *Anat. Rec.*, 81: 433–441.

AYKROYD, OLIVE E. 1938. The cytoplasmic inclusions in the oogenesis of man. *Z. Zellforsch.* 27: 691–710.

——, and J. BRONTË GATENBY. 1941. Cytology of human uterine glands in gravid and non-gravid phases. *Quart. J. Micr. Sci.*, 82: 541–562.

BACHMAN, RUDOLF. 1939. Über die Nebennierenrinde des Meerschweinchens während der Tragzeit. *Z. mikr.-anat. Forsch.*, 45: 157–178.

BAILLIF, RALPH N. 1941. Reaction of the rat omentum to injections of particulate matter. *Proc. Soc. Exp. Biol. Med.*, 47: 409–414.

BAKER, JOHN R. 1942. Some aspects of cytological technique. Chap. 1, *Cytology and Cell Physiology* (Ed., G. Bourne). Oxford: Clarendon Press.

——. 1944. The structure and chemical composition of the Golgi element. *Quart. J. Micr. Sci.*, 85: 1–71.

BAPTIST, B. A. 1941. The morphology and physiology of the salivary glands of Hemiptera-Homoptera. *Quart. J. Micr. Sci.*, 83: 91–139.

BARNETT, S. A. 1942. Observations on the distribution of ascorbic acid (vitamin C) in explanted cells. *J. Exp. Biol.*, 19: 88–91.

——, and G. BOURNE. 1941. The distribution of ascorbic acid (vitamin C) in the early stages of the developing chick embryo. *J. Anat.*, 75: 251–264.

——, and R. B. FISHER. 1943. Experiments on the silver nitrate method for the histological demonstration of ascorbic acid (vitamin C). *J. Exp. Biol.*, 20: 14–15.

BHATTACHARYA, D. B., and MURLI DHAR LAL SRIVASTAVA. 1939. The yolk nucleus of Balbiani. *Allahabad Univ. Studies, Zool. Sect.*, 1–11.

BEAMS, H. W. 1943. Ultracentrifugal studies on cytoplasmic components and inclusions. In *Frontiers in Cytochemistry* (Ed., Normand L. Hoerr), 71–90. Lancaster, Pa.: Jaques Cattell Press.

——, and R. L. KING. 1938. A study of the cytoplasmic components and inclusions of the developing guinea pig egg. *Cytologia*, 8: 353–367.

——, and J. F. SHEEHAN. 1941. The yolk nucleus complex of the human ovum. *Anat. Rec.*, 81: 545–557.

BENNETT, H. STANLEY. 1940. The life history and secretion of the cells of the adrenal cortex of the cat. *Amer. J. Anat.*, 67: 151–227.

——. 1941. Cytological manifestations of secretion in the adrenal medulla of the cat. *Amer. J. Anat.*, 69: 333–381.

BOURNE, GEOFFREY. 1942. Mitochondria and the Golgi apparatus. Chap. 4, *Cytology and Cell Physiology*. Oxford: Clarendon Press.

BUNO, WASHINGTON. 1938. L'appareil de Golgi de la cellule de Sternberg. *Bull. d'Histol. Appl.*, 15: 5–9.

CARTER, G. S. 1928. On the structure of the cells bearing the velar cilia of the nudibranch veliger. *J. Exp. Biol.*, 6: 97–109.

CHAMPY, C. H., AND R. COUJARD. 1939. Observations cytologiques et biologiques sur la spermatogénèse de quelques Batraciens et les caractères sexuels secondaires. *Arch. Zool. Exp.*, 81: 78–100.

CHATTON, E., and O. TUZET. 1941. Sur quelques faits nouveaux de la spermiogénèse du *Lumbricus terrestris*. *C. R. Acad. Sci. Paris*, 213: 323–376.

CLEMENT, R. 1938. On the cytoplasmic inclusions in the oogenesis of *Lepus cunniculus*. *Allahabad Univ. Studies*, 14: 137–174.

COPELAND, D. EUGENE. 1943. Cytology of the pituitary gland in developing and adult Triturus viridescens. *J. Morph.*, 72: 379–401.

COWDRY, E. V. 1938. *Textbook of Histology*. Philadelphia: Lea and Febiger.

DALTON, A. J., and J. E. EDWARDS. 1942a. Mitochondria and Golgi apparatus of induced and spontaneous hepatomas in the mouse. *J. Nat. Cancer Inst.*, 2: 565–575.

——, and ——. 1942b. Cytology of hepatic tumors and proliferating bile duct epithelium in the rat induced with p-dimethylaminoazobenzene. *J. Nat. Cancer Inst.*, 3: 319–329.

DAS, RAM SARAN. 1939. The cytoplasmic inclusions in the oogenesis of *Rhipcephalus sanguineus* (Latrielle). *Z. Zellforsch.*, 30: 36–51.

DAWSON, A. B. 1942. Some morphological aspects of the secretion process. *Federation Proc.*, 1: 233–240.

DEANE, HELEN W. 1944a. A cytological study of the diurnal cycle of the liver of the mouse in relation to storage and secretion. *Anat. Rec.*, 88: 39–65.

——. 1944b. A cytological study of storage and secretion in the developing liver of the mouse. *Anat. Rec.*, 88: 161–173.

DEHORNE, A. 1938. Formes sécrétantes du chondriome modifié. *C. R. Soc. Biol. Paris*, 128: 964–967.

——. 1939. Un exemple de modification du chondriome dans le sens d'un apport figuré à la prosécrétion. *C. R. Soc. Biol. Paris*, 130: 892–894.

DOOLEY, THOMAS P. 1941. The influence of colchicine upon the germ cells of insects (Orthoptera) with special reference to the mitochondria and dictyosomes. *Trans. Amer. Micr. Soc.*, 60: 105–119.

DORNESCO, TH. G. 1938. Sur la nature de l'appareil de Golgi des neurones des ganglions rachidiens des vertébrés. *C. R. Soc. Biol. Paris*, 129: 1232–1234.

DUMITRESCO, MARGUERITE. 1938. Les glandes séricigènes tubulaires de *Theridium tepidariorum*. *Arch. Zool. Exp.*, 79: 55–68.

EDWARDS, J. E., A. J. DALTON, and H. B. ANDERVONT 1942. Pathology of a transplantable spontaneous hepatoma in a C 3 H mouse. *J. Nat. Cancer Inst.*, 2: 555–563.

EMMEL, U. M. 1938. The Golgi apparatus in the proximal and distal tubule cells of the perfused frog's kidney. *Anat. Rec.*, 70: 371–384.

——. 1945. Alkaline phosphatase in the Golgi zone of absorbing cells of the small intestine. *Anat. Rec.*, 91: 39–47.

FALLER, ADOLPH. 1941. Histochemische Untersuchungen über das Vorkommen von Ascorbinsäure im Hoden und Nebenhoden von Ratten verschiedener Lebensalter. *Z. mikr.-anat. Forsch.*, 49: 333–358.

FEYEL, PIERRE, and JACQUES VARANGOT. 1938. Recherches cytologiques sur la glande thyroïde normale et pathologique (maladie de Basedow). *Ann. Anat. Path.*, 15: 136–164.

FEYEL, THERÈSE. 1939. Sur les constituants cytoplasmiques et sur l'évolution de la cellule acidophile dans la pars anterior de l'hypophyse du cobaye. *C. R. Soc. Biol. Paris*, 131: 560–562.

FILHOL, J. 1938. Recherches sur la nature des lépidosomes et les phénomènes cytologiques de la sécrétion chez les Gasteropods pulmonés. *Arch. Anat. Micr.*, 34: 155–218; 375–439.

——, and G. GARRAULT. 1938. La sécrétion de la prokératine et la formation de la capsule ovulaire chez les sélaciens. *Arch. Anat. Micr.*, 34: 105–145.

FISCHER, HERMANN. 1938. Das Verhalten des Golgi-Apparates in den Hauptstückzellen der Harnkanälchen bei experimentell gesteigerter und gehemmter Diurese. *Z. mikr.-anat. Forsch.*, 43: 342–361.

FOSTER, C. L. 1943. Studies on the parathyroid of the mouse. *J. Endocrinol.*, 3: 244–253.

GATENBY, J. B. 1943. A nuclear ring in the developing male germ cells of the dog and cat. *Nature, London*, 152: 79.

——, and L. COLLERY. 1943. Middle piece beads in the Cavia spermatozoon. *Nature, London*, 151: 253–254.

——, and J. D. SMYTH. 1940. The Golgi apparatus and pyrenoids of *Chilomonas paramecium*, with remarks on the identification of *Copromonas subtilis*. *Quart. J. Micr. Sci.*, 81: 595–617.

GIROUD, A. 1938. L'acide ascorbique dans la cellule et les tissus. *Protoplasma Monog.*, 16: 1–187.

GOORMAGHTIGH, N. 1940 Le cycle glandulaire de la cellule endocrine de l'artériole rénale du lapin. *Arch. Biol. Paris*, 51: 293–311.

GRAFFI, A. 1940. Intracelluläre Benzpyrenspeicherung in lebenden Normal- und Tuzmorellen. *Z. Krebsforsch.*, 50: 196–219.

GRESSON, R. A. R. 1940a. A cytological study of the centrifuged oocyte of the mouse. *Quart. J. Micr. Sci.*, 81: 569–583.

——. 1940b. Presence of the sperm middle piece in the fertilized egg of the mouse (*Mus musculus*). *Nature, London*, 145: 425.

GUTHRIE, MARY J., and KATHARINE R. JEFFERS. 1938. A cytological study of the ovaries of the bats *Myotis lucifugus* and *Myotis grisescens*. *J. Morph.*, 62: 523–557.

HIBBARD, HOPE. 1942. The Golgi apparatus during development in the stomach of *Gallus domesticus*. *J. Morph.*, 70: 121–150.

HIRSCH, G. C. 1938. Uber die Praesubstanz der Golgi-System. *Proc. Kon. Ned. Akad. Wet.*, 41: 840–846.

——. 1939a. Form- und Stuffwechsel der Golgi Korper. *Protoplasma Monogr.*, 18: 1–394.

——. 1939b. Einiges über die Restitution von Produkten in tierischen Zellen. *Vhl. dtsch. zool. Ges.*, 41: 255–295.

——. 1940a. Vitamin C und Golgi-Korper. *Protoplasma*, 34: 377–392.

——. 1940b. Over het aandeel van het vitamine C in de opbouw van producten in cellen. *Natuurwetenschap. Tijdschr.*, 21: 363–370. (seen only in *Biol. Abstr.*, 16: no. 690.)

——. 1940c. Der intraplasmatische Stoffwechsel in den Darmzellen von *Ascaris lumbricoides*. *Protoplasma*, 35: 280–288.

ITO, T. 1941. Über den Golgiapparat und die Mitochondrien der Spermatogonien sowie Spermatozyten des Menschen, nebst Bemerkungen der Riesenspermatogonien. *Cytologia*, 11: 436–451.

JAMES, EMORY S. 1939. The morphology of the thymus and its changes with age in the neotonous Amphibian (*Necturus maculosus*). *J. Morph.*, 64: 455–482.

JÄRVI, OSMO. 1939. Über die Restitution des Sekretstoffes in der grossen Unterzungendrüse der Katze, geprüft durch die Stufenuntersuchungsmethode. *Z. Zellforsch.*, 30: 98–155.

——. 1940a. Über die sogenannten "Lipochondrien" von Ries in der Pankreaszelle und ihre Beziehung zu den Pigmenten. *Z. Zellforsch.*, 31: 1–42.

——. 1940b. Die Beziehungen zwischen dem Vitamin C und der Golgi-Substanz im exokrinen Gewebe des Pankreas und in den Speicheldrüsen der Katze. *Protoplasma*, 34: 362–376.

——. 1940c. Entgegnung auf die Bemerkungen von G. C. Hirsch über meine Arbeit: Die Beziehungen zwischen dem Vitamin C und der Golgi-substanz. *Protoplasma*, 35: 274–279.

KEHL, R. 1939. Sur la polarité de l'appareil de Golgi dans les elements des tubes sexuels mÂles chez les Oiseaux. *C. R. Soc. Biol. Paris*, 131 104–106.

KIRKMAN, HADLEY, and A. E. SEVERINGHAUS. 1938 A review of the Golgi apparatus. *Anat. Rec.*, 70: 413–431, 557–573; 71: 79–103.

KRICHESKY, B., and H. MANDEL. 1943. The Golgi apparatus in uterine gland cells during pregnancy in the rabbit. *Univ. Cal. Pub. Zool.*, 47: 169–174.

LUDFORD, R. J. 1935. The cytological action of methylene blue. *Arch. exp. Zellforsch.*, 17: 339–359.

——. 1942. Pathological aspects of cytology. Chap. 8, Cytology and Cell Physiology (Ed., G. Bourne) *Oxford:* Clarendon Press.

MACLENNAN, R. F. 1939. Cytoplasmic inclusions. Chap. 3, Protozoa in Biological Research (Eds., G. N. Calkins and F. M. Summers). *New York:* Columbia Univ. Press.

——. 1940. A quantitative study of osmic acid impregnation in Protozoa. *Trans. Amer. Micr. Soc.*, 59: 149–159.

——. 1943. Centrifugal stratification of granules in the ciliate *Ichthyophthirius*. *J. Morph.*, 72: 1–25.

MAHONEY, FLORENCE JEROME. 1940. Spermatogenesis with special reference to certain extranuclear structures in the Pulmonate *Physa gyrina* Say. *Univ. Colo. stud. Gen. Sci.*, 26: 81–83.

MCCROAN, J. E., JR. 1940. Spermatogenesis of the crayfish, *Cambarus virilis*, with special reference to the Golgi material and mitochondria. *Cytologia*, 11: 136–151.

MCMANUS, J. F. A. 1943. Apparent reversal of position of the Golgi element in the renal tubule. *Nature, London*, 152: 417.

MEGLITSCH, PAUL. 1940. Cytological observations on *Endamoeba blattae*. *Univ. Ill. Biol. Mongr.*, 17: 1–140.

MILLER, RICHARD A., and OSCAR RIDDLE. 1942. The cytology of the adrenal cortex of normal pigeons and in experimentally induced atrophy and hypertrophy. *Amer. J. Anat.*, 71: 311–341.

MONNÉ, LUDWIK. 1939a. Polarizationsoptische Untersuchungen über den Golgi-Apparat und die Mitochondrien männlicher Geschlechtszellen einiger Pulmonaten-Arten. *Protoplasma*, 32: 184–192.

——. 1939b. Über die Farbenveränderung der Mitochondrien und des Golgi-Apparates im Dunkelfeld. *Arch. exp. Zellforsch.*, 23: 157–168.

NEEDHAM, JOSEPH. 1942. *Biochemistry and Morphogenesis*. Cambridge: Cambridge Univ. Press.

OKKELS, HARALD. 1934. Dynamic cytology of the thyroid gland. *Arch. exp. Zellforsch.*, 15: 343–347.

PALAY, SANFORD L. 1943a. The origin of neurosecretory granules from the nuclei of nerve cells in fishes. *Anat. Rec.*, 85: 331.

——. 1943b. Neurosecretion. V. The origin of neurosecretory granules from the nuclei of nerve cells in fishes. *J. Comp. Neur.*, 79: 247–274.

PARAT, MAURICE. 1928. Contribution à l'étude morphologique et physiologique du cytoplasme. *Arch. Anat. Micr.*, 24: 73–356.

PAYNE, FERNANDUS. 1942. The cytology of the anterior pituitary of the fowl. *Biol. Bull.*, 82: 79–111.

PEYRON, ALBERT, and GUY PUMEAU DELILLE. 1938. Sur la signification des cellules claires et des inclusions observées dans le papillo-épithéliome de Shope. *C. R. Soc. Biol. Paris*, 129: 1114–1116.

PFUHL, WILHELM. 1938. Über die funktionellen Beziehungen zwischen den Leberzellen und den Kupfferzchen Sternzellen. *Anat. Anz.*, 86: 273–295

——, and OSKAR DIENSTBACH. 1938. Die Speicherung und Verarbeitung von kolloiden Farbstoffen, Pigmenten und Lipoiden in der Golgi-Substanz der Leberzellen. *Z. Anat. Entwgsch.*, 108: 260–282.

POLLISTER, ARTHUR WAGG. 1939. The structure of the Golgi apparatus in the tissues of Amphibia *Quart. J. Micr. Sci.*, 81: 235–271.

PONSE, KITTY. 1938. Histophysiologie de l'activation thyroïdienne. *Rev. Suisse Zool.*, 45: 441–449.

POPPER, HANS. 1944. Distribution of vitamin A in tissue as visualized by fluorescent microscopy. *Physiol. Rev.*, 24: 205–224.

PORIS, ETHEL G. 1941. Studies on the endocrines of reptiles. II. Variations in the histology of the hypophysis of *Anolis carolinensis* with a note on the Golgi configuration in cells of the pars anterior and pars intermedia. *Anat. Rec.*, 80: 99–121.

RADSMA, W., and P. B. VAN WEEL. 1940. De Golgisubstantie in het schild-kliepithelium bij witte ratten in tropische en in koele omgeving Geneesk. *Tijdschr. Nederland.-Indie*, 88: 2858–2864. (Seen only in *Biol. Abstr.*, 15: no. 11755).

RATHNAVATHY, C. K. 1941. The spermatogenesis of *Clibanarius olivaceous* Henderson. *Proc. Ind. Acad. Sci. B.*, 13: 379–421.

RAURAMO, M., and E. TURPEINEN. 1940. Über die feineren Zellstrukturen bei Carcinoma corporis uteri. *Acta Soc. Med. Fennica Duodecim. B*, 29: 164–199. (Seen only in *Biol. Abstr.*, 17: no. 5033.)

REESE, J. D., and H. D. MOON. 1938. The Golgi apparatus of the cells of the adrenal cortex after hypophysectomy and on the administration of the adrenocorticotropic hormone. *Anat. Rec.*, 71: 543–556.

RICHTER, KENNETH M. 1940. A study of the cytoplasmic structures in the male germinal cells of several species of *Notonecta*, with special reference to the Golgi system. *J. Morph.*, 67: 489–522.

——. 1942. An experimental study of the cytology of human peripheral blood neutrophiles and lymphocytes. *J. Morph.*, 71: 53–76.

RINKEL, G. L., and G. C. HIRSCH. 1940. Die Restitution des Eiweiss-secretes zum Nestbau beim Stickling *Gasterosteus* in Verbindung mit dem Arbeitsrhythmus der Niere. *Z. Zellforsch.*, 30: 649–688.

ROBERTIS, E. DE. 1939. Action du jeûne prolongé sur la cytologie hépatique de *Bufo arenarum* (Hinsel). *C. R. Soc. Biol. Paris*, 130: 299–300.

——. 1941. The intracellular colloid of the normal and activated thyroid gland of the rat studied by the freezing-drying method. *Amer. J. Anat.*, 68: 317–337.

ROSKIN, G. R. 1938. Contribution à la cytophysiologie de la cellule musculaire lisse de l'Axolotl. *Bull. Histol. Appl.*, 15: 57–66.

ROSSMAN, ISADORE. 1940. The deciduomal reaction in the Rhesus monkey (*Macaca mulatta*). *Amer. J. Anat.*, 66: 277–342.

SALAZAR, A. L. 1936. Sur le système para-Golgien or système tannophile de la zone de Golgi, révélé par la méthode tanno-ferrique. *Arch. Anat., Histol., Embryol.*, 21: 65–95.

——. 1942. L'appareil para-Golgi et les conceptions actuelles sur la zone de Golgi. *Anat. Rec.*, 82: 309–326.

SATO, I. 1940. Studies on the cytoplasmic phenomena in the spermatogenesis of the oriental scorpion, *Buthus martensii*, with special reference to the structure of the chondriome ring and the dictyokinesis. *J. Sci. Hirosoma Univ. B*, 8: 1–116. (Seen only in *Biol. Abstr.*, 15: no. 14153.)

SESHACHAR, B. R. 1942. Origin of interlocular oocytes in male Apoda. *Proc. Ind. Acad. Sci. B*, 15: 278–279.

SIMPSON, WILLIAM L. 1941. The application of the Altmann method to the study of the Golgi apparatus. *Anat. Rec.*, 80: 329–343.

SINGH, B. N., and W. BOYLE. 1938. The vitellogenesis of *Gasterosteus aculeatus* (the stickleback) investigated by the ultracentrifuge. *Quart. J. Micr. Sci.*, 81: 81–108.

SLUITER, J. W. 1940. Die Cytologie, wahrend der ersten Phasen der Ovogenese, das Huhnereies. *Protoplasma*, 34: 393–430.

SMYTH, J. D. 1943. The Golgi apparatus in *Astasia harrisii*. *Nature, London*, 151: 110.

——. 1944. The Golgi apparatus of Protozoa. *Biol. Rev.*, 19: 39–47.

SOSA, J. M., and J. A. MENEGAZZI. 1940. The Golgi apparatus of striated muscle fibers of *Hirudo medicinalis* and its relation with contractile activity. *Arch. Soc. Biol. Montevideo*, 10: 6–14.

STEIN, K. F., ELIZABETH CALDWELL, and JEAN PETERS. 1942. Age changes in the anterior pituitary gland of the mouse. *Anat. Rec.*, 84: 523.

SUBRAMANIAM, M. K. 1938a. Studies on the structure of the Golgi apparatus. II. Liver cells of *Rhacophorus maculatus* Gray. *Proc. Ind. Acad. Sci.*, 7: 80–103.

——. 1938b. Studies on the structure of the Golgi apparatus. III. Some observations on the mechanism of secretion of the Golgi bodies in the intestinal cells of Lumbriconereis. *Proc. Ind. Acad. Sci.*, 7: 125–131.

——. 1939a. Studies on the structure of the Golgi apparatus. IV. Endostyle of *Branchiostoma indicum*. *Quart. J. Micr. Sci.*, 81: 429–450.

——. 1939b. Studies on the structure of the Golgi apparatus. V. The idiosome in the pancreas of the toad and its possible relation to ergastoplasm. *Proc. Ind. Acad. Sci.*, 9: 271–286.

TAKAO, S. 1939. Microchemical studies on the Golgi apparatus using protease-Nile blue sulphate techniques. I. The Golgi apparatus in hepatic cells in the mouse and newt. *J. Fac. Sci. Hokkaido Imp. Univ. Ser. VI*, 7: 1–16.

——. 1940. Microchemical studies on the Golgi apparatus using protease-Nile blue sulphate techniques. II. Golgi apparatus of pancreatic acinar cells of the mouse in fixed and living condition. *Cytologia*, 11: 261–281.

THOMPSON, D'ARCY. 1942. *On Growth and Form*. Second Ed. Cambridge: Cambridge Univ. Press.

TONUTTI, E. 1939. Über den Golgi-Apparat. *Vhl. Anat. Ges.*, 88: 78–81.

——. 1940. Die Vitamin-C-Darstellung im Gewebe und ihre Bedeutung zur funktionellen Analyse von Histosystemen. *Z. mikr.-anat. Forsch.*, 48: 1–53.

TURNER, JOHN B. 1940. Cytoplasmic inclusions in the ciliate *Tillina canalifera*. *Arch. Protistenk.*, 93: 255–272.

TUZET, O. 1938. Sur las spermatogénèse du *Buthus occitanus* (Amor). *Arch. Zool. Exp.*, 80: 335–351.

VAN TIEL, N. 1940. Der intraplasmatische Stoffwechsel in den Darmzellen von *Ascaris lumbricoides*. IV. Die Adsorption von Metallen an Golgi Korpern. *Protoplasma*, 35: 289–297.

VETTER, JOACHIM. 1940. Über die Frage der Beteiligung der Basalkörnten Zellen an den Resorptions- und Sekretionsvorgängen des Darmes. *Z. mikr.-anat. Forsch.*, 47: 33–48.

WALLRAFF, JOSEF. 1939a. Beiträge zur Morphologie und Morphogenese der Hypophysenzellen des erwachsenen Menschen. *Z. mikr.-anat. Forsch.*, 45: 631–667.

——. 1939b. Neue Untersuchungen an der menschlichen Hypophyse. *Vhl. Anat. Ges.*, 88: 94–95.

WATZKA, MAX. 1939. Vanänderungen des Golgi-Netzapparates nach Chloroformnarkose. *Z. mikr.-anat. Forsch.*, 46: 622–626.

WAUGH, J. G. 1942. Damage to the liver following sulphonamides. *Irish J. med. Sci., Ser. 6*: 607–610.

WEATHERBY, J. H. 1941. The contractile vacuole. Chap. 7, *Protozoa in Biological Research* (Eds., G. N. Calkins and F. M. Summers) New York: Columbia Univ. Press.

WEED, ISABELLE G. 1937. Cytological studies of developing muscle with special reference to myofibrils, mitochondria, Golgi apparatus and nuclei. *Z. Zellforsch.*, 25: 516–540.

WEEL, P. B. VAN. 1938a. Beiträge zur Histophysiologie des Dünndarmes. I. Zur Histophysiologie des absteigenden Dünndarmschenkels vom Reiher (*Ardea cinerea* L.). *Z. Zellforsch.*, 28: 62–82.

——. 1938b. Beiträge zur Histophysiologie des Dünndarmes. II. Zur Histophysiologie des Dünndarmes vom Frosch. *Z. vergl. Physiol.*, 26: 35–66.

——. 1939. Beiträge zur Histophysiologie des Dünndarmes. III. Die Veränderungen in den Darmdrüsenzellen während der Verdauung und in den Resorptionszellen während der Fettresorption. *Z. Zellforsch.*, 29: 750–777.

WELCH, G. STUART, and ALBERT C. BRODUS. 1940. Golgi apparatus of the thyroid gland. *Arch. Path.*, 29: 759–772.

WILSON, E. B., and A. W. POLLISTER. 1937. Observations on sperm formation in the centrurid scorpions with special reference to the Golgi material. *J. Morph.*, 60: 407–443.

WORLEY, ELIZABETH K. 1939. A study of the sperm-forming components in three species of Decapoda. *Cellule*, 48: 147–176.

WORLEY, LEONARD G. 1943a. The structure and function of the Golgi system in the living cells of developing molluscs. *Proc. Nat. Acad. Sci. Wash.* 29: 225–228.

——. 1943b. The relation between the Golgi apparatus and "droplets" in cells stainable vitally with methylene blue. *Proc. Nat. Acad. Sci. Wash.*, 29: 228–231.

——. 1944a. Studies of the vitally stained Golgi apparatus. II. Yolk formation and pigment concentration in the mussel *Mytilus californianus* Conrad. *J. Morph.*, 75: 77–101.

——. 1944b. Studies of the vitally stained Golgi apparatus. III. The methylene blue technique and some of its implications. *J. Morph.*, 75: 261–289.

——, and E. K. WORLEY. 1943. Studies of the supravitally stained Golgi apparatus. I. Its cycle in the tectibranch mollusc *Navanax inermis* (Cooper). *J. Morph.*, 73: 365–399.

THE EFFECTS OF CHANGES IN CHROMOSOME NUMBER ON AMPHIBIAN DEVELOPMENT

By G. FANKHAUSER

Department of Biology, Princeton University

"Many of the phenomena dealt with here, like polyploidy, in spite of the fact that they are of great significance for the general theory of genetics, are at present almost completely ignored by zoologists, as the phenomena are largely peculiar to the plant kingdom." Preface, Sansome and Philp (1932).

INTRODUCTION

ONE of the characteristics that should be included in the description of every species of plant or animal is the number of chromosomes that are to be found in its cells. Normally, each species has a definite, constant number of chromosomes which is maintained through all the cell divisions of the long and complex processes of development. The process of mitosis itself is admirably constructed to assure an equal division of each chromosome and to send a complete and identical complement of chromosomes into the two daughter cells. It is during the formation of the reproductive cells of the mature organism alone that we find a modified form of mitosis which automatically and with perfect regularity brings about a reduction of the chromosome number to one-half. The mature egg and sperm both carry the reduced or haploid number to the process of fertilization, and the fusion of the two half-nuclei preceding the first cell division of the egg restores the full or diploid chromosome number of the species. The diploid chromosome complement thus consists of two haploid sets, one contributed by each parent.

In view of the fact that the chromosomes carry the great majority of the known hereditary factors, the maintenance of the specific chromosome number becomes an essential feature: it assures an equal share of both parents in inheritance and is a prerequisite for the normal functioning of heredity, which is based on the presence of two complete sets of hereditary factors or genes in each cell of the embryo. It is obvious that it would be of great importance to know what would happen if some natural or experimental accident should interfere with the normal chromosome cycle and bring about a change in the chromosome number in the cells of the developing embryo; for instance, if an extra set of chromosomes should be added at the time of fertilization so as to give to the embryo all the genes in triplicate. Such accidents do occur in nature, and they can also be induced experimentally in the laboratory. The consequences of the presence of more than two chromosome sets, a phenomenon known as polyploidy, have been investigated extensively in plants, where this condition is normally of frequent occurrence and easily induced by various experimental procedures.

Among animals, polyploidy is supposedly a rather rare phenomenon in nature. To be sure, we do not find many groups of races or species which constitute a polyploid series, i. e., which differ from one another in chromosome number by one or more haploid sets, as is so often the case in plants. However, recent investigations have shown that polyploid individuals do appear spontaneously and not infrequently in diploid species, and that polyploidy may be induced by simple treatments of eggs at the time of fertilization. As a matter of fact, among larvae of salamanders the frequency of spontaneous changes in chromosome number appears to be higher than in most diploid species of plants, and the percentage of polyploid individuals produced by treatments with cold or heat is considerably greater than that obtained in similar experiments with plants.

The neglect of this field by the zoologists may be attributed in part to the fact that work on polyploidy in animals, in striking contrast to corresponding studies on plants, offers little promise of immediate practical applications in animal breeding, or of important theoretical contributions to the study of the mechanisms of evolution. In addition, there has also been a lack of those convenient techniques for the ready identification of polyploid individuals in life that are so important to the plant geneticists. Significantly, interest in the effects of changes in chromosome number in animals arose from work in experimental embryology and developmental genetics.

There are many reasons why it soon appeared very desirable to develop a definite program for the study of polyploidy in animals. On the one hand, many aspects of polyploidy that have been thoroughly investigated in plants require a comparative study on animal material, since the conditions and consequences of such unusual changes in the genetic system are not the same in all details, in spite of the general validity of cytological and genetical principles for both plants and animals. Even if it were merely to complete the general picture, information on a number of problems should be gathered: (1) the occurrence and frequency of polyploidy in different groups of animals; (2) the origin of these exceptional individuals, in other words, the mechanisms that are responsible for their production; (3) the effectiveness of methods for the experimental induction of polyploidy; (4) the general effects of polyploidy on cell size, body size, and viability, and on the general physiology and biochemistry of the organism; (5) the occurrence of qualitative effects, which are added to the more obvious quantitative consequences.

In addition to these aspects of general biological significance there are many which are of special interest to zoologists or which are peculiar to animals, such as the influence of polyploidy on embryonic and later development, on growth rate and final body size, and on the structure and physiology of various organs and tissues,—in particular, the circulatory and nervous systems and the endocrine glands.

Finally, there is one phase in which for obvious reasons animals have already played a more important rôle than plants, namely, the influence of polyploidy on sex determination, although in recent years these results have been confirmed or extended in research on dioecious plants. Even here, the zoological information is limited to a few species, while a general understanding of the sex-determining mechanisms calls for a much wider basis including the vertebrates.

Among the latter, the most favorable material for a study of polyploidy that combines cytological and embryological investigations is without doubt furnished by the amphibians, and the salamanders in particular, for several reasons:

(1) They possess large cells and large chromosomes, which are counted with relative ease.

(2) The chromosome number may be determined in whole-mounts of tailtips clipped from living larvae soon after hatching, a rapid method which equals or surpasses the roottip method of plant geneticists.

(3) By means of pituitary stimulation it is possible to obtain viable eggs during the greater part of the year; the larvae are easily raised to advanced stages, in some species to sexual maturity.

(4) The development of the amphibian egg has been most thoroughly investigated by descriptive and experimental methods, so that it will be possible to combine, later on, methods of experimental embryology with studies on polyploidy.

(5) Since species hybrids are easily obtainable in amphibians in certain combinations, it should not be difficult to induce polyploidy in cross-fertilized eggs, a technique which has yielded highly important results in plants.

(6) The occurrence of occasional triploid embryos in preserved material has been demonstrated by various investigators in different species of frogs and salamanders.

Because of the diverse aims of the investigations on polyploidy in amphibians, some of the problems outlined above have not been attacked so far, and none of the aspects have been analysed with any degree of completeness. However, a considerable amount of information has accumulated and will be reviewed in this paper. Particular emphasis will be placed on the effects of polyploidy and of other changes in chromosome number on embryonic and larval development. Comparisons with polyploid invertebrates and plants will be drawn whenever they appear to be of particular interest. For more complete reviews of the work on polyploidy in plants the reader is referred to the articles listed in the first section of the bibliography.

TERMINOLOGY

The term *polyploidy* was introduced by Winkler in 1916 (p. 422) to designate individuals with three, four, or more complete sets of chromosomes in place of the usual two sets. At the same time he proposed the more general term *heteroploidy* to cover any deviation from the normal diploid chromosome number, whether by whole chromosome sets or by one or more single chromosomes. The latter term deserves wider use, since it is the only one that includes polyploidy and haploidy, as well as irregular chromosome numbers. To distinguish between the deviations that involve complete sets and therefore conserve the normal balance between individual chromosomes, and those that produce irregular or unbalanced chromosome

combinations, Täckholm (1922) proposed the terms *euploidy* and *aneuploidy* which have been widely used by botanists.

A. METHODS OF IDENTIFYING LIVING HETEROPLOID INDIVIDUALS

1. Larvae

(a) Tailtip method

In many species of amphibians the fin surrounding the distal portion of the tail of the larva is thin enough to allow the preparation of whole-mounts in which the mitotic figures in the epidermis of the transparent fin may be studied with the oil immersion objective. Much of the classical work on mitosis was carried out on such preparations (Flemming, 1881–82, on *Salamandra*; Retzius, 1881, on *Triton*). Some of the first attempts to count the number of chromosomes were made on epithelial cells of the tailfin (Retzius, 1881). In the following year, Flemming (1882a) was able to determine the chromosome number in three cells of the buccal and gill epithelium of larvae of *Salamandra* as twenty-four but could not yet convince himself that this number might be constant for all the cells of the individual, and typical for the species.

The advantages of whole mounts of fin over sections of whole embryos or larvae for the determination of chromosome numbers were recognized early in the experiments on parthenogenesis, androgenesis, and related phenomena which produced haploid larvae (Bataillon, 1904; the Hertwigs, 1913; Levy, 1920a, b; Parmenter, 1933, 1940; and others). Either the chromosome number was determined directly by means of counts, or indirectly through measurements of the interphase nuclei, whose size increases roughly in proportion to the number of chromosomes which they contain. Later it was realized that portions of the tailfin, or the extreme tip of the tail itself, could be removed from living larvae, and their chromosome number determined while they proceeded with their development and, at the same time, regenerated the missing tissues (cf. Baltzer, 1922).

A simple method was thus available for the identification of the chromosome number of living amphibian larvae. All that was needed was to develop and apply it systematically to a large number of individuals in order to obtain information on the occurrence of spontaneous changes in chromosome number. The common Eastern newt, *Triturus viridescens*, was selected for the first investigations for three main reasons: (1) It offers considerable cytological advantages since the larvae have larger cells than those of many other species of salamanders, a thinner and more transparent tailfin with relatively few melanophores and little intra-epidermal pigment, and a diploid chromosome number of twenty-two (Fankhauser, 1932b) compared with twenty-four and twenty-eight in most other species. (2) The effects of haploidy had already been studied in this species by Kaylor (1937) in his experiments on androgenesis involving the removal of the maternal chromosomes in the second maturation spindle. (3) In preliminary experiments on androgenesis, two triploid embryos had been found among eleven preserved controls, demonstrating the not infrequent occurrence of exceptional polyploid individuals (Fankhauser and Kaylor, 1935).

The tailtip method was described in detail in an earlier paper in which the various evidences of polyploidy offered by the tailtip preparation were evaluated critically (Fankhauser, 1938c). Since then, the tailtip method has been applied successfully to several other species:

Triturus pyrrhogaster (2N = 24, fin less transparent because of more pigment; Fankhauser, Crotta, and Perrot, 1942).

Eurycea bislineata (2N = 28, smaller cells, fin less transparent because of thicker central layer of connective tissue, axis of the tailtip must be removed before mounting; Fankhauser, 1939).

Amblystoma mexicanum (axolotl, 2N = 28, smaller cells, more pigment except in larvae of the white or partial albino variety; Fankhauser and Humphrey, 1942).

Triturus torosus (Costello, 1942).

The summary of the technique given below applies to larvae of *Triturus viridescens* unless another species is mentioned.

The best stage for tail-clipping was found to be shortly after hatching (eighteen to twenty days at 20–22°C), when the fore limbs possess two prominent fingerbuds and show an indication of a third. At this stage, the yolk granules have disappeared from the epithelial cells of the tailfin; the number of mitotic figures is greater than in later stages (see Table 1); furthermore, several days elapse before the animals reach the feeding stage, so that it is possible to identify the heteroploid individuals in the meantime and to avoid wasting time feeding diploid larvae which are not to be kept as controls.

The larvae are anesthetized in a weak solution of chloretone (1:3000 to 1:5000); the posterior one-third (approximately) of the tail is amputated with fine scissors and dropped into Bouin's solution for from two to twenty-four hours. After a few hours in 70 per cent alcohol, the tailtip is stained in Harris' acid haemalum (diluted with 1 or 2 parts of water) for 3 to 4 minutes (depending on the age of the stain), washed for at least 20 minutes in several changes of tap water, dehydrated, cleared in xylene, and mounted in clarite (Fig. 4: 1–2).

The following criteria of changes in chromosome number may be used:

(1) Actual counts of chromosomes in epidermis cells at metaphase. Early metaphases usually present a polarview of the equatorial plate which is most satisfactory for counting (Fig. 4: 3–5). Later metaphases and anaphases are always seen in side view. If the original tailtip does not contain clear mitotic figures, as many as three additional tips with numerous mitotic figures may be obtained through regeneration from the same larva, at intervals of about two weeks (unpublished experiments of Rita C. Watson).

(2) Size of interphase nuclei. The nuclei of the epidermis are flat discs and show striking changes in size which are almost directly proportional to changes in chromosome number (Fig. 1). The nuclei of an unknown may be compared directly with those of a known diploid or triploid with the use of a comparison ocular. For more accurate study, twenty epidermis nuclei are drawn from the same region of each tailtip, and their total area is measured with a planimeter. Table 2 shows that this area increases rapidly between the haploid and triploid levels, but more slowly from there to the pentaploid level. The single measurement from a tetraploid individual is probably exceptionally large. In spite of considerable variations between individual tailtips, triploid larvae can be identified from such measurements if decisive chromosome counts should not be available.

In tailtips of axolotl larvae, the variations between nuclear measurements of individual tailtips with the same chromosome number are greater, so that there is considerable overlapping between the diploid and triploid ranges (Fankhauser and Humphrey, 1943, Table 1). Again, with higher chromosome numbers nuclear size increases more slowly. This may be explained in part by the fact that the thickness of the disc-shaped nuclei, as seen in optical section along the edge of the fin, remains practically constant up to the tetraploid chromosome number, but seems to show a slight increase in pentaploid cells (Fig. 3).

The nuclei of other tissues of the tailtip can also be used for comparison, although the differences between different levels of polyploidy are less striking in drawings of the largest optical sections through the nuclei because of their more rounded or oval shape (e. g., erythrocytes in capillaries of the fin, or in the small blood clot usually found at

TABLE 1

Number of metaphases in epidermis cells of tailtips amputated at different stages (approximately 24 hours apart). Twenty tailtip preparations of equal area were studied for each stage

STAGE	RANGE	AVERAGE
Third fingerbud indicated (F11).....	1–21	12
Third fingerbud flat (F12).....	1–17	7.5
Third finger bud prominent (F13)...	0–13	5.5
Larva begins to feed (F14).....	0–7	3
Later stages (development of 4th fingerbud, F15–F18).....		2

Note: The number of mitoses does not seem to vary significantly during a 24-hour period, a fact which had already been stated by Retzius (1881), working with the tailfin of *Triton* larvae.

Early in this work it became obvious that the external features of the embryonic development of *Triturus viridescens* differ sufficiently in details from those of *Amblystoma punctatum* and *Triton taeniatus* to make the use of Harrison's stages or Glaesner's normal tables impractical. In the construction of our own normal tables, which consist of brief descriptions, the development was first divided into periods that are designated by capital letters (B for blastula, G for gastrula, N for neurula, E for the following "embryonic" period, F for the subsequent period characterized by the development of the forelimb buds, and H for the final period covering the formation of the hindlimbs). Each period is divided into a series of numbered stages (e. g., F0 to F18, H0 to H14).

Following H14, the stage marked by the presence of a well formed fifth toe, little external changes are visible, aside from growth, until the first signs of approaching metamorphosis appear. There are altogether sixty-five stages, not including the early cleavages, which are designated by cell number.

The embryology of *Triturus pyrrhogaster* was again found to be sufficiently different from that of *T. viridescens* to necessitate the compilation of a different table based on the same principles.

TABLE 2

Area, in square inches, of twenty epidermis nuclei from tailtips of larvae of Triturus viridescens, drawn at a magnification of 630 ×

	HAPLOID	DIPLOID	TRIPLOID	TETRAPLOID	PENTAPLOID
Chromosome number	11	22	33	44	55
Number of tailtips used for measurements	4	17	16	1	8
Area of nuclei					
range	1.52–2.38	3.95–5.29	5.95–8.94	11.5	8.62–11.75
average	2.0	4.65	7.0	11.5	10.0
ratio	1.00	2.32	3.5	(5.7)	5.0

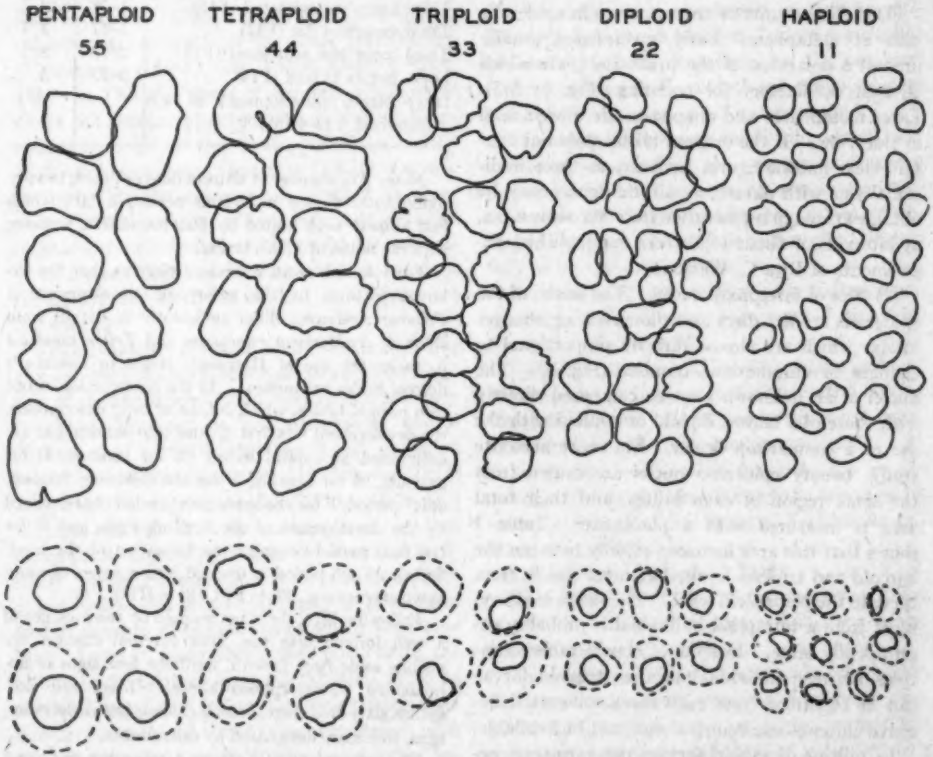

FIG. 1. RELATIVE SIZES OF NUCLEI AND CELLS FROM THE TAILFINS OF LARVAE OF TRITURUS VIRIDESCENS WITH DIFFERENT NUMBERS OF CHROMOSOME SETS

Above: Surface view of nuclei of epidermis cells. Nuclear size increases approximately in proportion to chromosome number. Below: Nuclei and cell boundaries of single gland cells (Leydig cells). Cell size increases with nuclear size. × 315.

the cut surface of the axis; nuclei of lateral line organs; muscle nuclei).

(3) The size of the cells, which is so useful in the detection of polyploid plants, cannot be used directly as a criterion because of the poor definition of the cell boundaries in most tissues. Exceptions are the erythrocytes and the gland cells (Leydig cells) in the epidermis (compare Fig. 1).

(4) Indirectly, the increased cell size is expressed in a wider spacing of the nuclei, which means a decrease in the number of nuclei per unit area. This is particularly obvious under the comparison ocular in the connective tissue layer of the fin (Fig. 4: 6–8).

(5) Since there is no significant increase in the body size of polyploid larvae, their organs are made up of a smaller number of larger cells. The decrease in number of cells or nuclei is often very plain in the lateral line sense organs (Fankhauser, Crotta, and Perrot, 1942, Figs. 7–8).

(6) In many species of plants, the number of nucleoli present in telophase or interphase nuclei is the same as the number of chromosome sets, since each nucleolus is formed at a localized region of a particular chromosome of each set ("nucleolar organizer"). The same relationship has been demonstrated in various species of animals, including amphibians (bibliography in Fankhauser and Humphrey, 1943). Among the salamanders studied so far, the species of *Amblystoma* are the only ones to show the nucleoli in the epidermal cells of the larval tailfin even without special staining methods, at least in some of the preparations. Although the numerical relationship is obscured in some of the nuclei through the fusion of nucleoli during interphase, the maximum number of nucleoli present always corresponds with the number of chromosome sets in the nucleus (Fankhauser and Humphrey, 1943, Figs. 1–8, Table 1). The value of this criterion is obvious, particularly in a species in which it is often difficult to obtain accurate chromosome counts.

Comparison of tailtip and roottip method: The tailtip of amphibian larvae has the great advantage of possessing a transparent fin, in which mitotic figures are accessible to the oil immersion objective in stained whole-mounts, without special treatment, while roottips cannot be used for chromosome counts without sectioning or smearing. Furthermore, while all the cells of the roottip are derived from one portion of the plant embryo, the radicle, the tailtip contains samples of cells from three widely separated regions of the amphibian embryo: most of the tissues originate from the material of the tailbud itself; the lateral line organs, however, grow out from a region behind the ear, and the blood cells originate in the blood island on the anterior ventral side of the embryo (cf. Fankhauser, 1938c, Fig. 6). Therefore, it is possible to test, in a single preparation, the chromosome condition of the embryo as a whole.

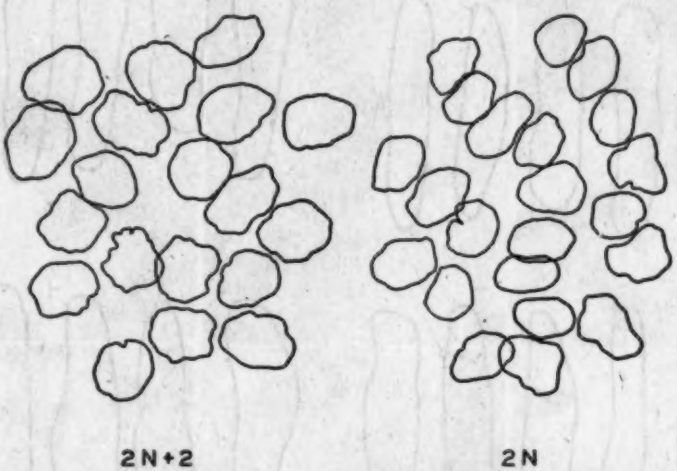

FIG. 2. NUCLEI OF EPIDERMIS CELLS FROM THE TAILFIN OF A HYPERDIPLOID LARVA OF TRITURUS VIRIDESCENS WITH 24 CHROMOSOMES (2N + 2) AND OF A NORMAL DIPLOID
Addition of two single chromosomes has caused a pronounced increase in nuclear size. × 315.

Detection of slight deviations in chromosome number. If the deviation from the normal chromosome number does not involve a whole set, actual chromosome counts are the only reliable means of identifying the heteroploid individual. However,

a larva of *Triturus viridescens* with 24 chromosomes (2N + 2) was first discovered because of a considerable increase in the size of the epidermal nuclei of the tailfin (Fig. 2). It seems that in amphibians as well as in *Drosophila* (Dobzhansky, 1929) and in *Crepis* (Shkvarnikov, 1934) some individual chromosomes may exert a relatively greater influence on nuclear size than others. Among the salamander larvae, the presence of unbalanced chromosome complements has so far always been associated with conspicuous abnormalities in development that have aided in the identification of these aneuploid individuals.

(b) Pigment pattern of young larvae

The changes in cell size and cell number induced by deviations from the normal chromosome number are often clearly expressed in the pigment pattern of the young larvae. The size of the individual melanophores may be used as an index of the chromosome number in many cases, although the differences in size between diploid and triploid melanophores, for instance, may be obscured by differences in their state of "contraction" or "expansion," which varies considerably from day to day. It is therefore important to compare also the number of pigment cells present in certain

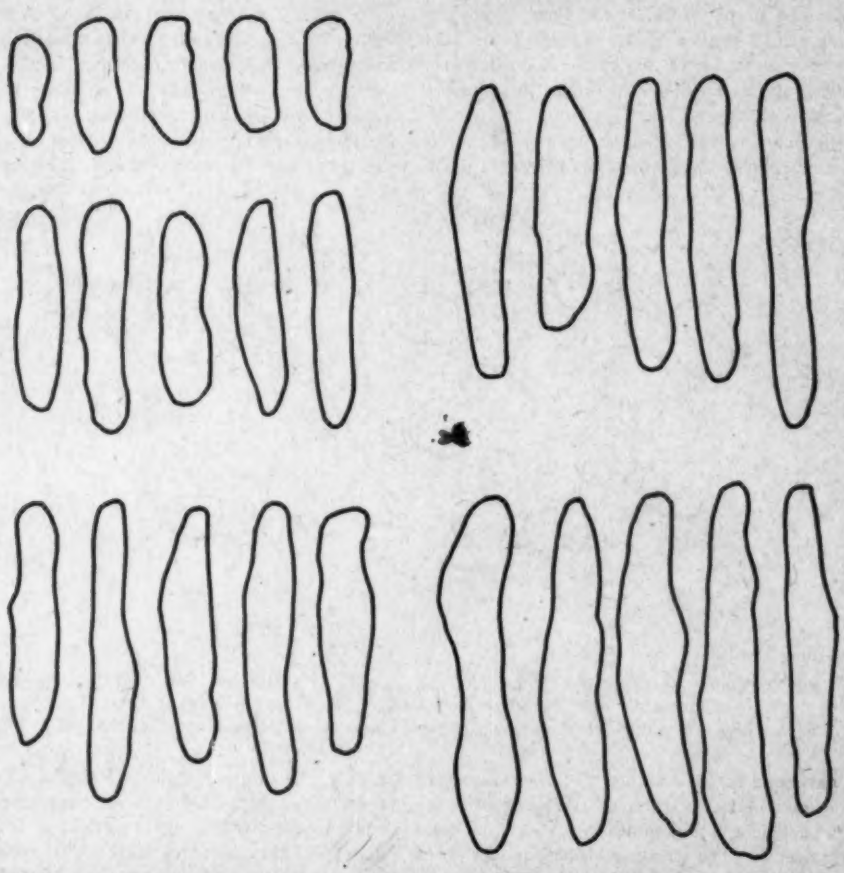

FIG. 3. OPTICAL SECTION THROUGH EPIDERMAL NUCLEI FROM EDGE OF TAILFINS OF AXOLOTL LARVAE
The nuclei are flat discs the thickness of which changes little with increasing chromosome number up to the tetraploid condition. On left: haploid, diploid, triploid. On right: tetraploid, pentaploid. × 1000.

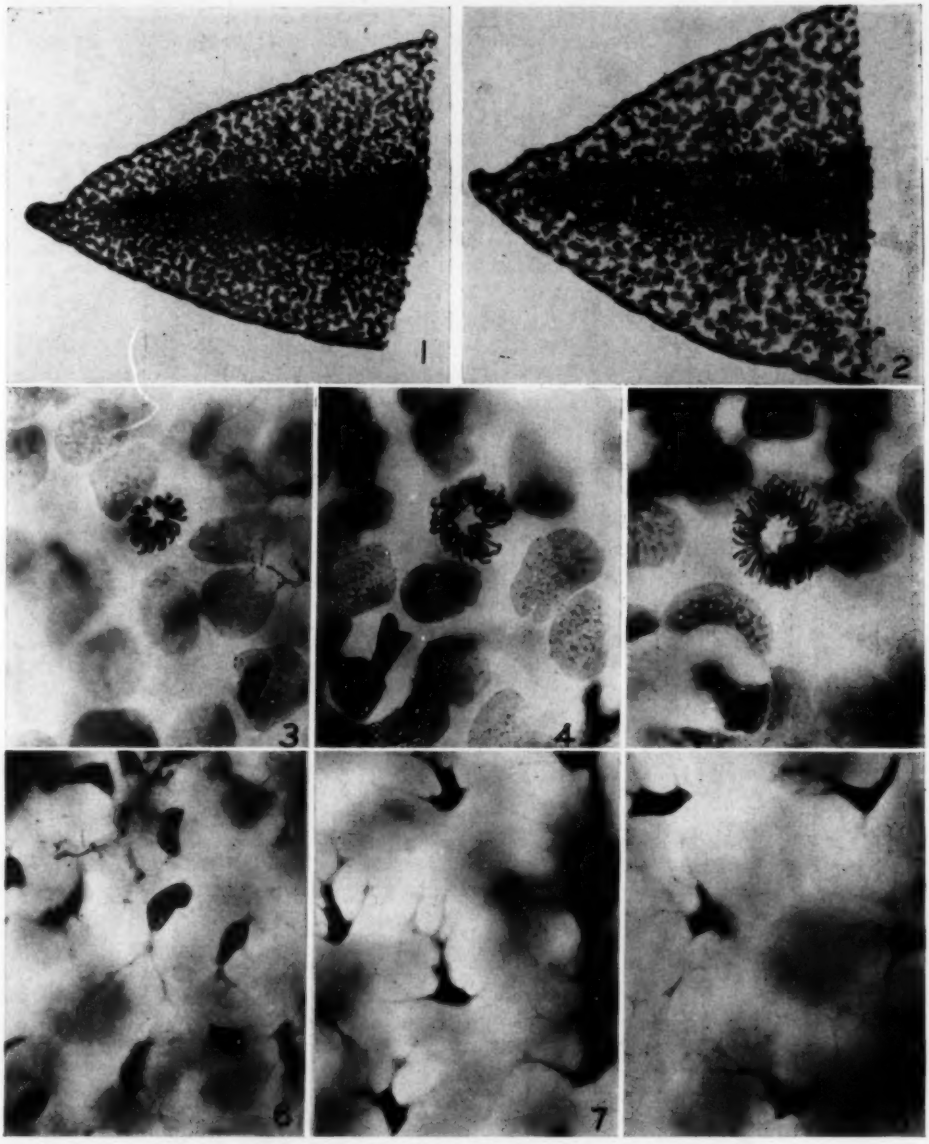

FIG. 4. TAILTIP PREPARATIONS OF LARVAE OF TRITURUS VIRIDESCENS

1: Whole mount of tailtip of a diploid larva, stained with Harris' acid hemalum. Note transparent fin with large, pale epidermal nuclei and small, darkly stained, and irregularly shaped nuclei of mesenchymal cells. In the axis of the tail the spinal cord appears as a dark line; above it, on the dorsal side, a series of lateral line sense organs. × 50.

2: Tailtip of a pentaploid larva. Nuclei and cells much larger. Cell boundaries not visible except in scattered gland cells near axis. Greater width of fin seems to be typical of pentaploid larvae. × 50.

3 to 5: Metaphases in epidermis cells in tailfins of diploid, triploid, and pentaploid larvae. The chromosomes are too long and too crowded to be counted in photographs. × 392.

6 to 8: Left to right: Connective tissue cells, from the mesenchymal layer supporting the tailfin, from a diploid, a triploid, and a pentaploid larva, respectively. The size and spacing of the nuclei increases with the chromosome number. The branching cytoplasmic processes, however, do not show any appreciable change in thickness. × 392.

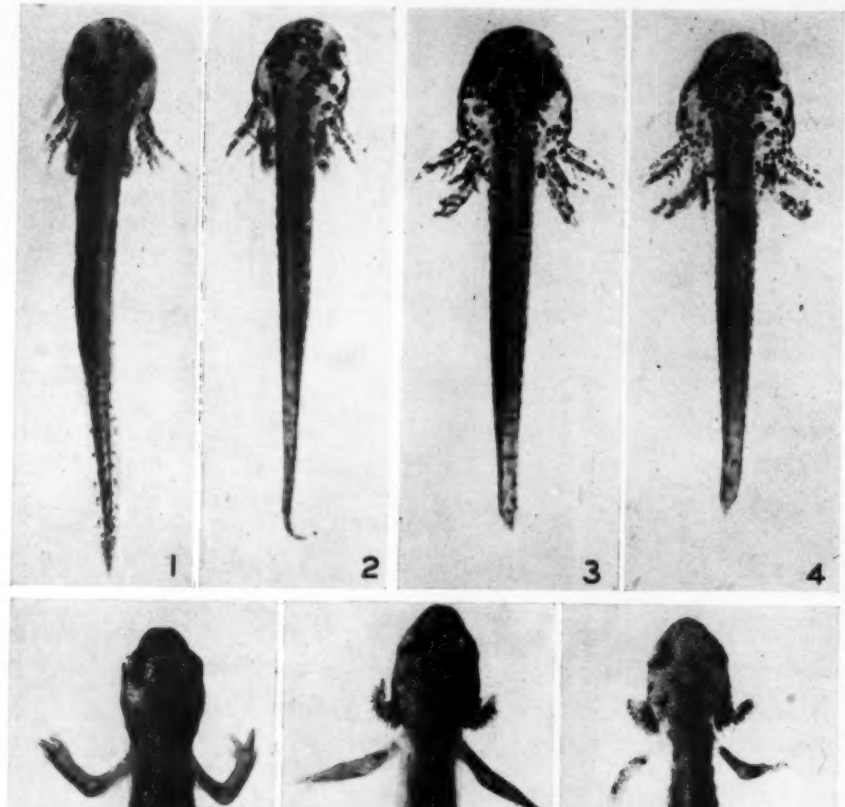

FIG. 5

areas like the head, the flank, and the tailfin. Since the body size of the larvae remains fairly constant at different levels of polyploidy, there are noticeably fewer pigment cells in the polyploids, in unit areas, than in the corresponding areas of diploids (Fig. 5: 1–4). In haploid larvae, on the other hand, although they are usually smaller from an early stage on, the increase in the number of melanophores per unit area is still very noticeable (Fig. 7).

In practice, all larvae are examined and classified with regard to their pigment pattern as early as possible. All suspicious looking animals are then tail-clipped for a cytological check, the result of which very often agrees with the prediction; of the larvae with unmistakably diploid pigment pattern only a small number are tail-clipped to furnish control preparations for comparison.

2. Metamorphosed and adult salamanders

In the laboratory, triploid salamander larvae have been found to be as viable as diploids in *Triturus viridescens* and *T. pyrrhogaster*. Since they occur spontaneously with considerable frequency (see Table 3) some of these, at least, should grow to adult size under natural conditions. Up to the present, a single adult triploid has been discovered, a male newt (*Triton taeniatus*) found by Böök (1940) in Sweden. In a large collection of testes fixed for a reexamination of spermatogenesis, one pair contained triploid spermatogonia and, during various stages of meiosis, showed the typical irregularities of triploid organisms. The body of the animal had not been preserved; presumably it was triploid throughout.

Polyploid adults might be detected in life by the following methods: (1) determination of nuclear and cell size in pieces of shed skin; (2) determination of nuclear size, and perhaps chromosome counts, in sections or in whole mounts of epidermis from the amputated tip of the tail, and, later, from the regenerating tailtip; (3) measurements of the size of erythrocytes in blood smears made at the time of amputation.

The last-mentioned method was put to a preliminary test by Michalski (1942) with large larvae and adults of *Eurycea bislineata*. The blood samples were diluted with physiological salt solution and studied immediately under a cover glass ringed with vaseline. The living erythrocytes vary from 32 to 37 micra in length, with an average of 33.4 micra, and from 19 to 21 micra in breadth, with an average of 20 micra. Of 117 animals studied, all possessed red blood cells within the normal range of variation of diploid individuals and were therefore presumably all diploid.

In tailtip preparations of newly hatched *Eurycea* larvae the nuclei and cell bodies of erythrocytes are strikingly larger in triploids (Fankhauser, 1939, Fig. 18). In young axolotl larvae, the erythrocyte nuclei of triploids average 15 micra in length, compared with 12.7 micra in diploids (Fankhauser and Humphrey, 1942). It should thus be possible to identify triploids among adults, unless the initial difference in cell size is reduced in the adult through a process of regulation.

B. Addition or Subtraction of Whole Chromosome Sets (Polyploidy and Haploidy)

1. Frequency of spontaneous aberrations

Earlier occasional observations by several investigators indicated that triploid individuals occur not infrequently among normal embryos raised from eggs that were not subjected to any experimental treatment (G. and P. Hertwig, 1920, *Rana esculenta*; Dalcq, 1930, *Rana fusca*, *R. esculenta*; Fankhauser, 1934c, *Triton palmatus*; Fankhauser and Kaylor, 1935, *Triturus viridescens*; cf. Fankhauser, 1938c, Table 1). These exceptional embryos were identified after fixation by chromosome counts in sections. Unless the

FIG. 5. TRIPLOID AND TETRAPLOID LARVAE OF TRITURUS VIRIDESCENS AND CONTROLS

1 and 2: Young diploid (left) and triploid larvae after precocious removal from jelly capsules (stage F8, forelimb buds notched, several days before tailclipping). The presence of larger but fewer pigment cells (melanophores) on the head is the earliest visible criterion of triploidy. × 10.

3 and 4: The same larvae one week later, after removal of tailtips (stage F12, flat third finger bud). Maximal expansion of menalophores, which partly obscures the difference in pigment pattern. × 10.

5 and 6: The same animals at the age of about 3 months. The diploid has completed metamorphosis and left the water: note blunt snout, bulging eyes, almost complete disappearance of gills, black pigment spots formed by clusters of melanophores, few white pigment spots on left side of body which turn vermilion later on. The triploid, slightly longer, is entering metamorphosis (first molt layer shed in part, black spots forming, gills slightly reduced, eyes beginning to bulge, snout still larval in shape). × 3.

7: Tetraploid larva (the only one found so far in this species) at metamorphosis, 4½ months old. Body size approximately normal. Single melanophores scattered between black spots clearly larger than in 6. Coiling of tail and pointed snout appear to be typical for animals with more than three sets of chromosomes. × 3.

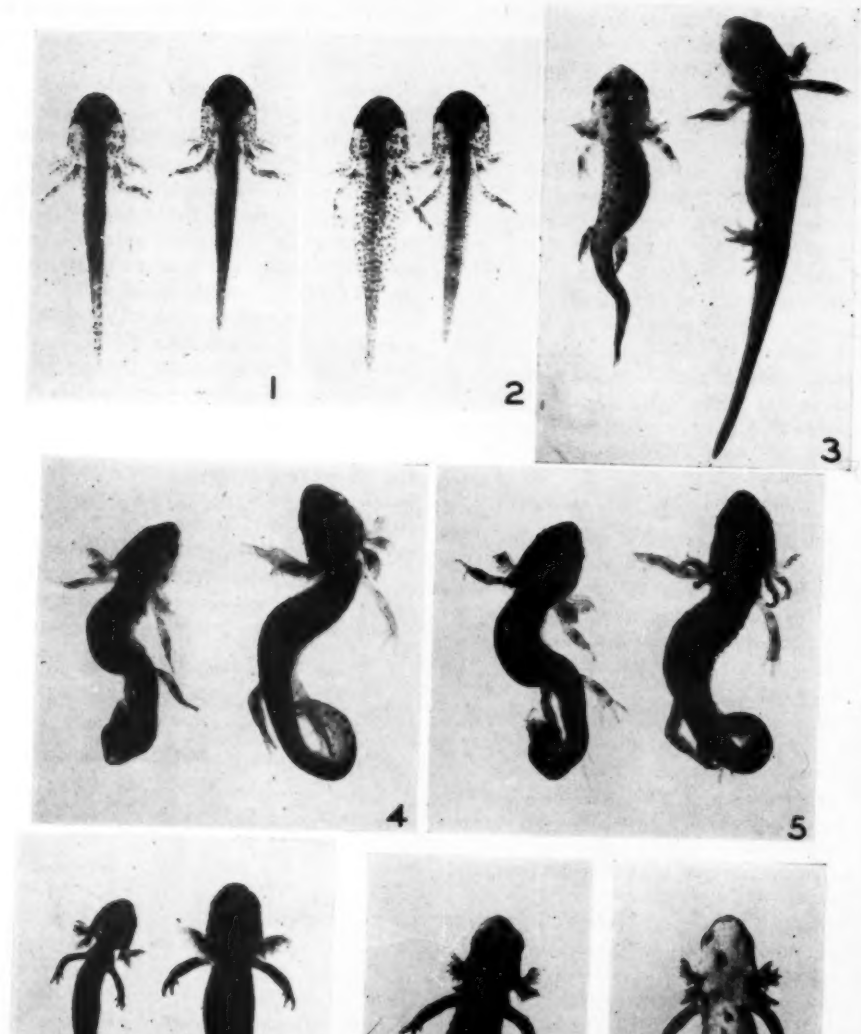

FIG. 6

viability of the embryos is greatly decreased by the deviation in chromosome number, such exceptional individuals should still be present among the young larvae at the time of hatching, when they may be identified in life by the tailtip method described earlier.

Beginning in November 1937, a systematic search for exceptional heteroploid individuals among young larvae of *Triturus viridescens* has been carried out, with the collaboration of several graduate and undergraduate students. While the normal breeding period is in the spring, egg-laying may be induced from late October on by implantation of two anterior lobes of frog pituitary, given two days apart (Kaylor, 1937). On the approach of the normal breeding season, the dose may be decreased to one or one-half a lobe to avoid overstimulation and deposition of large numbers of unfertilized eggs on the bottom of the culture dish. Since the adult females usually carry a store of spermatozoa in the spermatheca from the fall mating season, the eggs are fertilized in normal fashion as they are laid singly on leaves of *Elodea*. Eggs which are attached to the bottom of the aquarium very rarely are fertilized.

Since the time of the last detailed report (Fankhauser, 1941b), the total number of larvae that have been classified with regard to chromosome number has been more than doubled (Table 3). From the outset of these observations it appeared that triploidy is the predominating type of spontaneous heteroploidy, occurring with the relatively high frequency of 1.8%. This percentage varies greatly with different matings and may thus be influenced by genetic factors; the highest proportion of triploids produced by any female was eight among a total of 29 larvae, or 27.6 per cent (unpublished observations of W. T. Powers).

It was expected that tetraploid larvae would occupy the second place in frequency; however, only a single tetraploid larva has been found so far, as contrasted with seven pentaploids (0.28%). It is interesting to note that in January, 1943, two pentaploid larvae were obtained from a group of 34 untreated eggs laid by one female during one day.

In view of the numerous experiments on the induction of haploid development in amphibian eggs of various species, carried out by many investigators during the past thirty years, as well as the striking appearance of the haploid larvae, it is surprising that spontaneous haploids were not discovered until 1940/41, when they first appeared among larvae of three species of salamanders, *Triturus viridescens*, *Triturus pyrrhogaster*, and *Eurycea bislineata* (a lungless salamander of the family Plethodontidae). Since then more haploid larvae have been found in the first mentioned species and also among larvae of the axolotl.

Compared with deviations involving whole chromosome sets, aneuploid or unbalanced aberrations adding or subtracting one or more single chromosomes seem to be rare. Only two such larvae have been discovered so far in *Triturus viridescens*. The actual frequency of embryos with aneuploid chromosome complements may be considerably higher, for two main reasons: (1) slight deviations in chromosome number cannot be discovered as a rule except by counts in particularly clear metaphase plates that are free from crowding and overlapping of chromosomes; and (2) the disturbance of the genic balance in aneuploids may lead to abnormal development and death at an early embryonic stage, long before the tailtip test can be applied; actually, both the hyperdiploid and the hypo-diploid larva were strikingly abnormal and unviable.

FIG. 6. PENTAPLOID ANIMALS AND CONTROLS

1: Pentaploid (left) and diploid larvae of *Triturus viridescens*, 3½ weeks old (stage F17, flat fourth finger bud), 5 days after amputation of tailtips. Melanophores contracted. Pentaploid normal except for pigment pattern and slightly larger size. × 4.5.

2: Same animals, 5½ weeks old (stage HO, first appearance of hindlimb buds). Body cavity of pentaploid extended with fluid (ascites). Melanophores expanded. × 4.5.

3: Another pentaploid larva (left) approaching metamorphosis, 4½ months old, with a triploid animal in a similar stage. Note small size, S-shaped curvature of body axis, and pointed head of pentaploid. × 1.8.

4: Two other pentaploid larvae at age of 102 days, approaching metamorphosis. Animal on right nearly normal in size. Both show strong curvature of body axis and coiling of tail. × 2.1.

5: The same two pentaploids 8 days later. The animal on right has shed the first molt layer; gill branches and tailfin much reduced. All external metamorphic changes normal, including formation of black and white (later vermilion) pigment spots. × 2.1.

6: Pentaploid (left) and diploid larvae of *Triturus pyrrhogaster* at the age of 3 months, showing difference in growth rate. The diploid larva entered metamorphosis shortly afterwards. Body axis of pentaploid shows slight curvature. × 1.6.

7 and 8: Dorsal and ventral views of the same pentaploid as in 6, at age of 4¾ months. Beginning of metamorphosis (one day before first molt). The animal has reached approximately normal body size and shows a more pronounced curvature of tail. × 1.6.

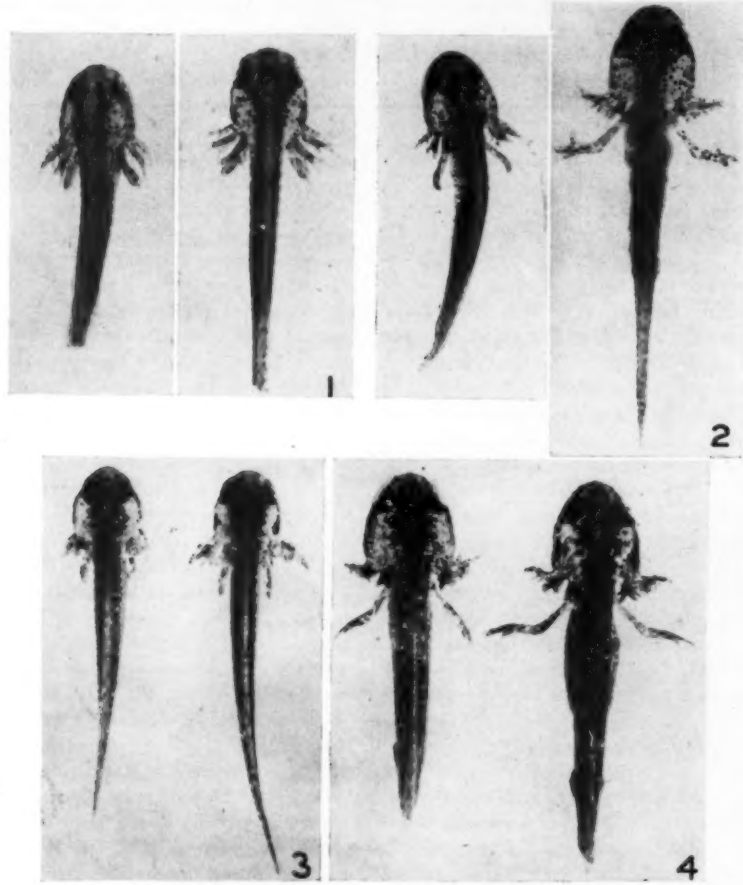

FIG. 7

A third group of rare aberrations includes chromosome mosaics, larvae in which different chromosome numbers, e. g., haploid and diploid, are present in different parts of the body. Haploid and diploid cells may be equally abundant, or one type may predominate; they may show a bilateral distribution with a clear line of demarkation coinciding for the greater part with the median plane of the larva, or they may be irregularly mixed so that most of the organs are composed of both types of cells. Again this type is probably more frequent than would appear from Table 3, since in most cases they are discovered only when the tip of the tail itself has a mosaic constitution. When the cells of one chromosome constitution are more numerous than those of the other, the condition is not recognized, as a rule, except by a careful study of sections through the preserved animal.

Less extensive investigations on the occurrence of spontaneous polyploidy have been carried out on larvae of the Japanese newt, *Triturus pyrrhogaster* (Fankhauser, Crotta, and Perrot, 1942; and unpublished observations made in 1944), and of the two-lined salamander, *Eurycea bislineata*. In the former, the frequency of spontaneous triploidy seems to be similar to that in *Triturus viridescens*. In *Eurycea bislineata* it is considerably higher, although not as high as was indicated by the first observations that demonstrated the existence of 13 triploids and 2 tetraploids among 134 larvae (Fankhauser, 1939). Later, Michalski (1942) identified 15 triploids, 2 haploids, and 3 haploid/diploid mosaics among 412 larvae. As in *Triturus viridescens*, the proportion of triploid larvae produced varies with different females; perhaps it is also influenced by other, as yet unknown conditions.

In 1942, the investigations on polyploidy were

TABLE 3

Frequency of spontaneous changes in chromosome number among young larvae of four species of salamanders

	TRITURUS VIRIDESCENS (2N = 22) NOV. '37–JUNE '44	TRITURUS PYRRHOGASTER (2N = 24) 1940/41, '44	EURYCEA BISLINEATA (2N = 28) 1938/39, '40/42	AXOLOTL (2N = 28) 1942–44
Total number of larvae examined	2448	398	546	over 3000
Diploid	2387	392	511	
Triploid	44 (1.8%)	4 (1%)	28 (5.1%)	1
Tetraploid	1	—	2	1
Pentaploid	7 (0.28%)	1	—	2
Haploid	4 (0.16%)	1	2	7
Hyper-diploid (2N–2)	1	—	—	—
Hypo-diploid (2N–3)	1	—	—	—
Mosaics:				
haploid/diploid	1	—	3	2
haploid/triploid	1	—	—	—
diploid/hyper-triploid	1	—	—	—

FIG. 7. HAPLOID LARVAE AND CONTROLS; HYPER-DIPLOID LARVA

1: Spontaneous haploid larva (left) of *Triturus viridescens*, developed from an untreated egg, and a diploid at the same stage of development (F12, flat third finger bud). Haploid 3 weeks old, diploid slightly younger. Haploid slightly shorter (appears much shorter because of removal of a larger portion of tail than in diploid). Pigment cells smaller and more numerous, eyes smaller. × 7.

2: The same animals 2 weeks later. The haploid (left) has reached the final stage of its development. It has fed little, shows reduction of gills, fusion of digits, increasing curvature of body, and mild ascites. × 7.

3: Haploid larva (left) of *Triturus pyrrhogaster*, developed from a refrigerated egg, and control, 18 days old, before amputation of tailtips. Haploid easily identified by small, numerous melanophores. × 5.6.

4: The same larvae, 39 days old, shortly after second amputation of tail. The haploid (left) is practically normal in size and general appearance, except for the pigment pattern. It had previously fed well but suddenly refused all food and was preserved five days later. × 5.6.

5: Another cold-induced haploid larva (left) of *Triturus pyrrhogaster* and its control, 31 days old. The haploid shows the characteristics of most haploid amphibian larvae: dwarfing, edema, microcephaly. It never fed. × 5.6.

6: Highly abnormal hyper-diploid larva (right) of *Triturus pyrrhogaster* (27 or 28 chromosomes = 2N + 3 or 4) and control of same age. Extreme microcephaly and edema are the most striking features. × 5.

extended to axolotl larvae, in collaboration with R. R. Humphrey of the University of Buffalo. The primary aim of this line of work has been the experimental induction of triploidy in combination with breeding experiments, and the analysis of the influence of triploidy on sex. No systematic check of all untreated larvae for the presence of aberrant chromosome complements was attempted, except in the first series of experiments where a single triploid was found among 148 larvae (Fankhauser and Humphrey, 1942). The other heteroploid larvae listed in Table 3 were picked out from a large number of controls because of their striking appearance, particularly with regard to the pigment pattern. This accounts for the absence of additional spontaneous triploids, since the differences in pigment pattern between triploid and diploid larvae are rather slight in this species, so that experimentally induced triploids often remain unidentified until the tailtip preparations have been studied.

Possible influence of pituitary-induced ovulation on the frequency of heteroploidy

With the exception of the axolotl, most of the observations listed in Table 3 were made on material obtained by pituitary stimulation of the females. The artificially induced ovulation might conceivably be responsible, at least in part, for the frequent production of abnormal chromosome numbers. However, it can be shown that aberrations occur with approximately equal frequency during the winter and during the normal breeding season, in spite of the difference in the amount of stimulation required to produce egg-laying. Furthermore, heteroploid larvae have been obtained from eggs of *Triturus viridescens* laid in the laboratory by unstimulated females. This, of course, does not prove conclusively that populations of young larvae collected in their natural habitat contain as high a proportion of individuals with abnormal chromosome numbers. This necessary test cannot be carried out with larvae of *Triturus viridescens*, since the eggs of this species are laid singly on water plants and the chances are slight that any number of eggs or young larvae could be collected. With other species which deposit the eggs in batches, such as *Amblystoma* and *Eurycea*, the test should not be difficult.

Comparison with other animals and with plants

No accurate figures are available for the frequency with which occasional polyploid individuals appear in other species of animals. In *Drosophila*, Morgan, Bridges, and Sturtevant (1925, p. 161) stress the "very high frequency for the occurrence of triploidy." This statement is based on the fact that within five years from their discovery in 1920 "intersexes of the triploid type have been found 15 times and there have been seven discoveries of triploid females originating de novo from diploid lines." However, the total number of individuals classified during this period must have been very large, and more recent rough estimates made by several *Drosophila* workers in personal conversation put the actual frequency of triploidy well below one per cent. We do know, however, that a completely haploid *Drosophila* has not been seen yet, although a number of haploid/diploid mosaics are on record.

In plants, the frequency with which polyploid and haploid individuals appear spontaneously has been recorded in relatively few cases only. The figures that have come to my attention are listed in Table 4; a wider search of the literature would undoubtedly produce others. A glance at the table shows that, in the majority of species, triploids appear with a frequency considerably below one per cent. The frequency is increased when one or both of the parents are trisomic, i. e., when they carry an extra chromosome. An exceptional case has been recorded by Shull (1929) in *Oenothera* where 12 per cent triploids appeared in one family. The cause of this unusual behavior could be traced to the mother, which produced an unusually high proportion of unreduced eggs. The proportion of spontaneous haploids in maize, in the jimson weed, *Datura*, and in the snap-dragon, *Antirrhinum*, the three species in which the most extensive counts were made, is one in 2000 or lower. Compared with these frequencies in plants, heteroploid salamander larvae occur with impressive abundance.

2. The origin of spontaneous aberrations in chromosome number

(a) Triploidy

Triploid individuals arise through the union of an unreduced, diploid gamete with a normal, haploid one. The third chromosome set may thus be contributed by either parent. If the parents differ in genetic constitution, the appearance of the triploid offspring may tell where the additional chromosome set came from. In plants it seems to be furnished usually by the egg, perhaps for the

very simple reason that the pollen tubes produced by diploid pollen grains often burst when growing in a normal, diploid style. In the one clearly established case of paternal origin of the extra chromosome set, in maize (Rhoades, 1936), it seems more likely that two haploid sperm nuclei, rather than a single, diploid nucleus, fused with a haploid egg nucleus (dispermy).

larvae of purely maternal character appear which must have developed from diploid eggs (G. Hertwig, 1918, etc.; Tchou-Su, 1931, 1936). One female of *Rana esculenta*, when crossed with a male *Bufo viridis*, produced false hybrids which were all diploid; eggs of the same female fertilized by sperm of its own species gave rise to triploid tadpoles (G. and P. Hertwig, 1920). Tchou-Su (1936) showed

TABLE 4

Frequency of spontaneous polyploidy and haploidy in plants

SPECIES	AUTHOR	CHROMOSOME NUMBER	FREQUENCY	REMARKS
Maize	Einset, 1942, 1944b	triploid	3 in 1916	Offspring from cross between trisomic and diploid plants
		haploid	2 in 1916	
	Randolph, 1941	haploid	ca. 1 in 2000	
	Randolph and Fischer, 1939	parthenogenetic diploid	23 in 17,165 (ca. 1 in 750)	in tetraploid race
Datura	Satina, Blakeslee, and Avery, 1937	haploid	73 in ca. 410,000 (0.018%)	
Antirrhinum majus	Knapp, 1939	haploid	ca. 1 in 2000	
Tomato	Lesley and Lesley, 1930	triploid	3 in ca. 9000 6 in ca. 2000	from diploid parents from trisomic parents
Cucumis	Shifriss, 1942	tetraploid	1 in ca. 25,000	
		parthenogenetic diploid	8 in 800	in tetraploid race
Apple	Einset, 1944a	triploid	2 in 278	
		tetraploid	1 in 278	in a much larger population the frequency has since been found to be lower (Einset, 1944b)
Crepis capillaris	Navashin, 1925	triploid	1 in 150	Sudden rise in temperature suggested as cause of relatively high frequency
		pentaploid	1 in 150	
Oenothera	Shull, 1929	triploid	19 in 148 (12%)	in one family only; the average frequency is considerably lower

In triploid animals, genetic criteria have not been available so far to decide directly the question of their origin. However, some evidence has been furnished by experiments on cross-fertilization between different species of frogs and toads in which the penetration of the foreign spermatozoon stimulates the egg to divide but the sperm nucleus does not take part in development ("gynogenesis"). Such eggs give rise to "false hybrids" that are usually haploid; occasionally, however, diploid

that, in crosses between Chinese species of anurans, diploid false hybrids develop from eggs which did not give off the second polar body. On the other hand, Bataillon and Tchou-Su (1929, fig. 24) described an unfertilized egg of *Bufo calamita* in which the second maturation spindle contained the diploid number of dyads.

Unreduced gametes of either type may originate in various ways, primarily (1) from tetraploid oocytes or spermatocytes in animals, from tetra-

ploid mega- or microsporocytes in plants, through normal meiosis, and (2) through disturbances of meiosis in normal, diploid cells.

(1) The literature contains numerous reports on the occurrence of groups of tetraploid cells in the first meiotic division, or in pre-meiotic divisions, in diploid plants and animals, including man (Painter, 1923). Sometimes polyploid germ cells occur with surprising frequency, as in the grasshopper, *Rhomalea microptera*, where Mickey (1942a, b) found cells showing various degrees of polyploidy in each follicle studied. A similar condition observed in barley has been traced to the presence of a recessive factor which causes the formation of a variable proportion of "multiploid" microsporocytes (L. Smith, 1942).

In amphibians, tetraploid cells have been seen in the testis of frogs (Levy, 1920a). A preliminary study of testes of *Triturus viridescens* and *Eurycea bislineata* has demonstrated so far the existence of a few giant, presumably tetraploid, spermatocytes in a single testis of the first mentioned species. It seems clear that diploid spermatozoa could not be produced in this way in sufficient number to account for the occurrence of almost two per cent triploid larvae. An instance of normal maturation of a tetraploid oocyte is probably given by the diploid egg of *Bufo calamita* mentioned above. More information on the chromosome number of ovarian eggs should be obtainable by counting the bivalents in isolated germinal vesicles.

(2) Disturbances of meiosis in diploid cells (failure of synapsis, suppression of the first or second maturation division) leading to the formation of diploid gametes in animals and diploid spores in plants have been described frequently. In amphibians, diploid eggs are formed occasionally through suppression of the second maturation division, as is shown by Tchou-Su's observations mentioned earlier. That triploid embryos may originate spontaneously in this way is also indicated by the fact that triploidy may be easily induced by cold or heat treatment of salamander eggs during the second maturation division.

(b) Tetraploidy

Tetraploid zygotes may result from the chance meeting of an exceptional unreduced egg and an exceptional unreduced sperm, an accident which should be very rare. In *Drosophila*, fertilization of a triploid egg by a haploid sperm has been suggested as a possible origin of the rare tetraploid females, because hexaploid sectors have actually been seen in gonads of triploid individuals from which triploid eggs should arise by normal meiosis.

In the silkworm, *Bombyx*, genetic evidence indicates that tetraploid females may originate by fertilization of triploid eggs by haploid spermatozoa; in this species, however, the triploid condition of the eggs seems to be derived from the fusion of the egg nucleus with two haploid polar nuclei, rather than by normal maturation of hexaploid oocytes (Hasimoto, 1934).

Doubling of the diploid chromosome number during the first division of the zygote, following normal fertilization, would also produce tetraploid embryos ("somatic doubling"). Evidence concerning the relative importance of these various possibilities in the production of the rare spontaneous tetraploids among salamander larvae is lacking.

(c) Pentaploidy

The formation of pentaploid zygotes can be interpreted most easily as the result of a fusion between a tetraploid and a haploid gamete. A tetraploid gamete may originate in various ways, e. g., by suppression of both maturation divisions and inclusion of all tetrads in a single nucleus, or by suppression of the second maturation division in a cell which was already tetraploid at the beginning of meiosis. Navashin (1925) suggested suppression of both maturation divisions, producing a tetraploid gamete, as the most probable origin of his pentaploid individual of *Crepis capillaris*. The predominance of individuals with odd numbers of chromosome sets among salamander larvae, compared with the scarcity of tetraploids, clearly shows that accidents leading to changes in chromosome number happen much more frequently during meiosis than during the early divisions of the zygote.

(d) Haploidy

The great majority of haploid plants are purely maternal in appearance and therefore parthenogenetic in origin. Paternal, androgenetic haploids do occur, however. In *Antirrhinum*, for instance, Knapp (1939) found a ratio of 0.05 per cent maternal haploids to 0.005 per cent paternal ones.

During the past year observations on haploid axolotl larvae derived from crosses between genetically different races have produced some evidence regarding their mode of origin (Humphrey and Fankhauser, unpublished). A mating between a homozygous dark female and a recessive

white male produced one haploid larva which was white and must therefore have developed with a paternal set of chromosomes, i. e., by androgenesis. Other matings have indicated, although less conclusively, that haploid embryos may also originate by gynogenesis, or possibly parthenogenesis. Additional information from black by white crosses should tell soon which of the two types of accident leading to haploidy is actually more common.

(c) The possible rôle of polyspermy

Polyspermy, which was mentioned as the mechanism producing triploidy in maize in one case, may also be involved in salamanders, where it is actually a natural or "physiological" phenomenon. However, the supernumerary spermatozoa present in the majority of the eggs are effectively prevented from taking part in development, so long as their number remains small (Fankhauser, 1932a; Fankhauser and Moore, 1941a). The maximum number tolerated by the egg, and the stage to which the accessory spermatozoa develop before degenerating vary considerably between different species. In spite of the existence of an inhibiting mechanism, it is not improbable that an extra set of chromosomes may be contributed by an accessory sperm nucleus in rare cases.

3. Experimental induction of changes in chromosome number

In spite of the relatively high frequency with which heteroploid salamander larvae appear spontaneously, it would take many years to collect enough information on the influence of various abnormal chromosome complements on development. Obviously it would be very useful to have methods by means of which some types of heteroploidy could be induced experimentally, similar to the procedures that have been used by plant geneticists in recent years with so much success. Among zoologists interest in such techniques was limited for a long time to those inducing haploidy, since this whole line of investigation began with the classical experiments on parthenogenesis with eggs of frogs, which were followed by studies on gynogenesis, androgenesis, and merogony in amphibians in general. All these modifications of the normal process of fertilization typically lead to the formation of haploid embryos, although other deviations in chromosome number, including polyploidy, may be obtained as occasional by-products whose origin is usually unknown. It was not until 1939 that the experimental addition of a third chromosome set to the normal diploid complement became possible, while the problem of inducing higher levels of polyploidy in amphibian eggs has not been solved at present.

(a) Haploidy

The various methods that may be used for the production of haploid amphibian larvae were reviewed a few years ago. Since the mature gametes are haploid, all that is needed is to preserve this condition in the egg as it begins its development. This may be accomplished basically by four routes (cf. Fankhauser, 1937a, frontispiece):

(1) by stimulating the haploid, unfertilized eggs to development by artificial means, e. g., by pricking with a needle—*parthenogenesis*;

(2) by fertilizing normal eggs with spermatozoa that had been treated previously with an agent which incapacitates the sperm chromosomes without suppressing sperm motility (radiations, chemicals such as trypaflavine, sodium fluoride)—*gynogenesis*;

(3) by fertilizing eggs the chromosomes of which have been damaged previously by radiation or removed by operative techniques, with normal spermatozoa, so that development takes place with the sperm nucleus alone—*androgenesis*;

(4) by dividing the egg shortly after fertilization in such a way that one fragment contains the egg nucleus, the other the sperm nucleus; the former fragment, as a rule, does not make more than an attempt at development, since in the majority of cases the isolated egg nucleus divides abnormally or not at all—"*gyno-merogony*" (Fankhauser, 1937b); the fragment with the sperm nucleus usually divides and may give rise to a haploid larva—"*andro-merogony*."

More recently haploid larvae have been obtained accidentally by treating fertilized eggs with cold (Fankhauser and Griffiths, 1939, Griffiths, 1941, *Triturus viridescens*; Fankhauser, Crotta, and Perrot, 1942, *Triturus pyrrhogaster*; Costello, 1942, *Triturus similans*; Fankhauser and Humphrey, 1942, axolotl; see Table 5); with heat (*Triturus pyrrhogaster*, unpublished, see Table 7); or with hydrostatic pressure (Rugh and Marsland, 1943, *Rana pipiens*). In such cases it is usually not known whether development took place by androgenesis or gynogenesis. A single haploid larva of the axolotl, out of a total of 26 haploids found among 1017 larvae developed from refrigerated eggs has given evidence of its origin. Since it was derived from a mating between a recessive white

female and a heterozygous dark male and itsel showed dark pigmentation, it must have developed androgenetically (Humphrey and Fankhauser, unpublished).

There is indirect evidence that gynogenesis may also take place in cold-treated amphibian eggs. Eggs of toads (*Bufo*) and tree frogs (*Hyla*) fertilized by spermatozoa of frogs (*Rana*) do not develop beyond the blastula stage when raised at room temperature. However, if they are cooled to 0°C for 5 to 20 hours shortly after insemination, some of them pass through gastrulation and develop into larvae most of which are haploid (Rostand, 1933, 1934, 1936). The low temperature apparently prevents the fusion of the egg and sperm nuclei, with the result that the egg nucleus alone takes part in development. It is possible that a similar inhibition of the sperm nucleus by the cold treatment also takes place in some eggs that had been fertilized by sperms of the same species.

Possibility of parthenogenetic development in salamander eggs. The eggs of frogs and salamanders, although they are very similar in their general appearance, differ markedly in some phases of their earliest development. Fertilization of frog's eggs is strictly monospermic under normal conditions, and the entrance of a single additional spermatozoon makes normal development impossible. In salamanders, on the other hand, the majority of the eggs are polyspermic to a varying degree, but the accessory sperms are prevented by some inhibitory mechanism from dividing and thus disturbing the normal progress of cleavage. The two types of eggs also differ in their reaction to agents inducing parthenogenesis. Puncture with a fine needle is effective with the frog's egg, but completely ineffective with that of *Triton taeniatus* (Bataillon and Tchou-Su, 1929, p. 806). Negative results with eggs of other species of salamanders are not conclusive because of the small number of experiments performed. However, salamander eggs may respond better to other treatments inducing parthenogenesis. Böök (1941) mentions the fact that treatment at +1.4° to +2.8°C for four to seven hours induced cleavage in three out of four unfertilized eggs of *Triton taeniatus*, although their development did not proceed beyond the gastrula stage. Bataillon (1904) had been able to obtain development up to the gastrula stage in eggs of *Rana fusca* exposed first for half an hour to 35°C, then raised at 15–16°C in 6 per cent cane sugar. Recent experiments with unfertilized eggs of *Triturus viridescens* (Wagner, 1944) showed that exposure to 36°C for 25 to 33 minutes, whether or not it was followed by a short cold treatment, induced development to blastula or gastrula stages without treatment with cane sugar solution in a considerable number of cases. One of these eggs gave rise to an embryo the chromosome number of which has not been checked as yet. In other eggs exposed to the same treatment, incomplete furrows were formed. Exposure to cold alone (+2°C) for several hours produced attempts at cleavage in a varying proportion of eggs, but no blastulae.

The problem of the origin of diploid parthenogenetic or gynogenetic larvae. The great majority of parthenogenetic frog tadpoles are dwarfed, weak, and unviable. However, ever since the beginning of the experiments of traumatic parthenogenesis occasional tadpoles have appeared which were normal, vigorous, and on examination of their cells were found to be diploid. The possible origin of these diploid individuals has been discussed many times and at great length. The most recent reviews may be found in Rostand (1938), Kawamura (1939a), Parmenter (1940), and Tyler (1941). This problem is of interest here because it is closely connected with that of the origin of triploid and other polyploid individuals from fertilized eggs. The various possibilities may be classified into three groups:

(1) doubling of the chromosome number by an initial monastral, anastral, or abnormal amphiastral mitosis of the haploid egg nucleus, followed by normal mitosis. Such a process should produce delay in the appearance of the first cleavage detectable in the living egg;

(2) complete suppression of the first or second maturation division, or retention of the haploid set normally eliminated in the second polar body, indicated in the living egg by the failure of the first or second polar body to appear;

(3) production of a diploid egg from a tetraploid oocyte through normal meiosis, a process to which no clue could be found in the appearance of the living egg.

The majority of diploid tadpoles whose cleavage histories are known originated from eggs showing a delay in the appearance of the first cleavage furrow corresponding to one or two nuclear divisions. This suggests, although it does not prove, an origin of the diploid chromosome number according to one of the routes mentioned under (1). The cases with undelayed cleavage may have originated by any of the accidents listed under (2) and (3). Bataillon and Tchou-Su (1929) pointed out that

diploid eggs might occur spontaneously with sufficient frequency to account for the origin of all diploid parthenogenetic tadpoles.

That suppression or revocation of the second maturation division, which has reached the metaphase stage at the time of fertilization or treatment, may play a rôle is indicated by the observations of Rostand (1934, 1938) on cross-fertilized eggs of toads and frogs. Refrigeration of the freshly fertilized eggs not only induced gynogenesis, as mentioned above, but also a great rise in the proportion of viable diploid tadpoles that appeared among the expected haploid ones. Presumably the cold treatment which incapacitated the foreign sperms also caused the retention of the second polar body in some of the eggs.

(b) Triploidy

Cold treatment. The first method for the induction of triploidy in normally fertilized amphibian eggs was suggested by Rostand's experiments on cross-fertilized eggs of toads and frogs discussed earlier. If prolonged refrigeration of these eggs fairly often produces diploid, gynogenetic tadpoles through suppression of the second maturation division, similar treatment of normally fertilized eggs should lead to the production of triploid embryos.

The first experiments were carried out by Griffiths in 1938 with eggs of *Triturus viridescens* and demonstrated at once the effectiveness of this simple method. If the eggs were transferred to a constant temperature bath kept at from 0° to +3°C within a few minutes after fertilization and treated for from five to twenty-four hours, the great majority of the larvae developing from the treated eggs were found to be triploid (Fankhauser and Griffiths, 1939; Griffiths, 1941). If, on the other hand, refrigeration was delayed for thirty minutes, it was no longer effective. By that time the second maturation division, which in *Triturus*, as in other amphibian eggs, is arrested in metaphase until fertilization takes place, has progressed to late anaphase (Fankhauser and Moore, 1941a) and can no longer be stopped by the low temperature.

Since 1939 the refrigeration method has been applied to many more eggs of *Triturus viridescens*, as well as to eggs of four other species of salamanders (Table 5). The productiveness of this treatment is remarkable, particularly in *Triturus viridescens*, where 78 per cent of all the larvae so far obtained from refrigerated eggs were found to be triploid. The low number of triploids obtained by Costello with eggs of *Triturus similans* may be explained by his statement that the treatment began at various times after laying; in many cases it was probably too late to prevent the normal formation of the second polar body. In Böök's experiments with eggs of *Triton taeniatus*, the relative inefficiency of the treatment may have been caused by the fact that after the exposure to cold, he allowed the temperature to rise slowly from about 1.4° to 21°C. In our laboratory the eggs are transferred abruptly from room temperature to the cold bath and back, since the investigators who have used extreme temperatures for the induction of polyploidy in plants seem to agree that the rapid change in temperature, the shock, is more important in producing the desired effect on mitosis than the actual temperature employed. Special experiments to test this point have not yet been carried out.

On the other hand, eggs of different species also differ in their reaction to the same cold-treatment, as a comparison of the results obtained with *Triturus viridescens*, *T. pyrrhogaster*, and the axolotl indicates. Moreover, although eggs of the same species are given what may be considered the optimum treatment, different series of experiments will give different percentages of triploid larvae, largely because the eggs deposited by different females differ in their response to cold. Those of a considerable number of females of *Triturus viridescens* have yielded 100 per cent triploids, while those of others produced less than 33 per cent. This difference cannot be explained by the fact that females from different localities were used in the experiments, as has been suggested before (Fankhauser, 1942, p. 28); but the possibility that the eggs react differently to the same treatment in the winter and spring has not been ruled out completely so far.

Differences between individual females tested at the same time are very pronounced in the axolotl, where the eggs of certain females were found to be completely refractory to refrigeration and produced 100 per cent diploid larvae.

It would be interesting to know the complete range of low temperatures that are capable of inducing triploidy. The experiments carried out so far do not demonstrate a simple relation between degree of temperature and percentage of triploids produced (Table 6). As a whole, temperatures above 4°C are clearly less effective, but some triploid larvae have been obtained with treatments at a temperature slightly over 6°C.

The effect of variations in the duration of the

TABLE 5

Summary of results of refrigeration experiments with eggs of several species of salamanders

Temperature: 0° to 4.35°C.
Duration of treatment: usually from 5 to 24 hours (cf. Table 6).

SPECIES	NUMBER OF EGGS TREATED	NUMBER OF LARVAE OBTAINED	CHROMOSOME NUMBER			
			triploid	diploid	haploid	others
Triturus viridescens (results of all experiments performed from 1938 to 1944)	509	264	202 (78%)	50	4	7 haploid/diploid mosaics 1 haploid/triploid
Triturus pyrrhogaster (Fankhauser, Crotta, and Perrot, 1942)	117	29	13 (44.8%)	11	4	1 hyperdiploid (2N + 3 or 4)
Triturus similans (Costello, 1942)	?	100	13	81	4	2 haploid/diploid mosaics
Triton taeniatus (Böök, 1941, 1944)	129	57	5	50	2*	—
Axolotl (Fankhauser and Humphrey, 1942, and current exp.)	?	1017	347 (34%)	633	26	1 tetraploid 3 pentaploid 3 hypodiploids (2N − 3 or 4) 2 haploid/diploid mosaics 1 triploid/pentaploid 1 diploid/pentaploid

* Three additional haploids were found among the non-viable embryos.

TABLE 6

Effectiveness of temperatures over 4.35°, and of different durations of treatment at 2°C, in inducing triploidy in eggs of Triturus viridescens

(Fankhauser, 1942, Table V, and current experiments of W. T. Powers)

TEMPERATURE	DURATION OF TREATMENT	NO. OF LARVAE OBTAINED	CHROMOSOME NUMBER		
			triploid	diploid	others
4–5°C	5 to 24 hours	14	1	12	1 haploid/diploid mosaic
5.5°C	5 to 24 hours	14	5	9	
5–6.5°	5 to 24 hours	9		9	
6.38°	5 to 24 hours	26	6	20	
Total: 4°–6.38°	5 to 24 hours	63	12	50	1 haploid/diploid mosaic
2°C	30 to 50 min.	3	3	—	
	1 to 2 hours	3	3	—	
	3 to 4 hours	6	6	—	
	4 to 5 hours	5	5	—	
	5 to 7½ hours	16	16	—	
	16½ to 21 hours	21	21	—	

treatment has also been studied. From the beginning of the experiments it did not seem to make much difference whether eggs of *Triturus viridescens* were refrigerated for five or for twenty-four hours, while a few shorter treatments produced diploid larvae only. However, current experiments of W. T. Powers have shown that cooling for thirty minutes may be sufficient to interfere with the second maturation division (Table 6).

Cold treatment may also induce haploidy in some cases, as has been discussed before, and, more rarely, other deviations in chromosome number, particularly haploid/diploid mosaics. Aneuploid larvae and higher polyploids appear also, but so rarely that they may well represent spontaneous aberrations which were in no way influenced by the treatment.

The mortality among treated eggs varies with the species and, even under the best circumstances, approaches 50 per cent. These figures are not too reliable, since it is not always possible to recognize those treated eggs that failed to develop because they were unfertilized. In *Triturus viridescens*, where the most extensive observations on the early development of treated eggs are available, mortality is highest during early cleavage. The chromosomal condition of such eggs and of more advanced non-viable embryos has not yet been investigated and may show some interesting abnormalities.

Cytological studies of fertilization and early cleavage in refrigerated eggs begun by E. Rogers were interrupted by the war. They will demonstrate the exact nature of the primary effect of the cold treatment. In the meantime it may also be possible to determine directly by observations on living eggs whether or not the second polar body fails to appear, although the polar bodies are not always easily seen in newt eggs, and very small exovates of the size of polar bodies are not infrequently present.

Heat treatment. High temperatures of 38° to 50°C have been used extensively for the induction of polyploidy in plants, both during the maturation divisions and after pollination, during the early divisions of the zygote, to obtain somatic doubling (cf. Fankhauser, 1942, Table 1). Exposure of freshly laid eggs of *Triturus viridescens* to temperatures varying from 35 to 37°C for from five to over fifty minutes was found to be just as effective in inducing triploidy as prolonged refrigeration (Fankhauser and Watson, 1942). These observations have since been confirmed and extended (Table 7). Variations in the duration of the treatment show that the mortality of the eggs rises rapidly with exposures lasting over thirty minutes (Table 8). The ten-minute treatment has been adopted tentatively as the standard exposure because of the lower rate of mortality compared with longer exposures, and because of the higher proportion of triploids produced as compared with five-minute treatments (Erdman and Thompson, 1943).

A single pentaploid larva has been obtained so

TABLE 7

Summary of results of heat experiments with eggs of Triturus viridescens and Triturus pyrrhogaster

TEMPERATURE AND DURATION OF TREATMENT	NO. OF EGGS TREATED	NO. OF LARVAE OBTAINED	CHROMOSOME NUMBER		
			triploid	diploid	others
Triturus viridescens					
35 to 37°C, 5 to over 50 minutes (Fankhauser and Watson, 1942)	104	58	49 (84.5%)	9	—
36°, 5 to 25 minutes (Erdman and Thompson, 1943)	74	55	33	21	1 pentaploid
36–37°, 10 minutes (M. Criscitiello, unpublished)	23	8	4	4	—
Total		121	86 (71 %)	34	1
Triturus pyrrhogaster					
36–37°C, 10 minutes (unpublished)	24	7	1	4	2 haploids

far in these experiments. It may well have been of spontaneous origin. However, pentaploid larvae may be expected to appear in such experiments if any of the eggs were tetraploid before meiosis. Untreated, such eggs would produce spontaneous triploids; following experimental suppression of the second maturation division they should give rise to pentaploid embryos.

The mortality among heat-treated eggs reaches its highest value during the blastula stage, rather than during early cleavage as in refrigerated eggs. Cytological study of sectioned material will show whether the two types of treatment actually produce different cytological abnormalities that lead to a standstill of development at two distinct periods.

On return to a normal temperature the arrested cells recover rapidly but frequently show multipolar anaphases; tetraploid cells are rare.

A similar reaction of earlier stages of development to cold is indicated by recent experiments of Böök (1944). Of 64 eggs of *Triton taenialus* treated more than thirty minutes after fertilization but before the first cleavage, thirteen developed normally to neurulae. Study of sections showed that they were complex chromosome mosaics; this condition is designated by Böök as "multiform aneuploidy" and must have arisen as a consequence of multipolar mitoses. Exposure of neurulae to cold produced arrest of metaphases, followed by the formation of restitution nuclei with an increased number of chromosomes.

TABLE 8

Effectiveness of different durations of heat treatment (35–37°C) in inducing triploidy in eggs of Triturus viridescens

AUTHOR	DURATION	NO. OF EGGS TREATED	NO. OF LARVAE OBTAINED	CHROMOSOME NUMBER		
				triploid	diploid	others
	minutes					
Fankhauser and Watson, 1942 (table 3)	5–9	7	5	5	—	
	10–19	47	34	29	5	
	20–29	24	12	8	4	
	30–over 50	26	7	7	—	
Erdman and Thompson, 1943	5	18	15	6	8	1 pentaploid
	10	43	33	23	10	
	20	10	6	3	3	
	25	1	1	1	—	

A few experiments with eggs of *Triturus pyrrhogaster* carried out this spring showed that the heat treatment also produced chromosomal deviations, including haploidy, in this species; the high rate of mortality among treated eggs is not necessarily an indication of a greater susceptibility of *T. pyrrhogaster* eggs to heat, since it was also unusually high among the untreated controls.

(c) Higher degrees of polyploidy

If cold or heat, when applied during the second maturation division, induce triploidy, the same treatments given during the first cleavage mitosis should inhibit the separation of the chromosomes at anaphase and produce tetraploid embryos. Barber and Callan (1943) studied the effects of cold on mitosis in the tailfin of newt larvae and in spermatogonia of adults and found that the spindle is abnormally developed or completely suppressed.

Preliminary experiments with heat treatments of eggs of *Triturus viridescens* at various times between fertilization and the beginning of the first cleavage produced negative results. This may be explained largely by the fact that it is difficult to time the treatment properly, since the interval between insemination and beginning of anaphase, as determined from sections through preserved eggs, varies considerably between individual eggs kept at the same constant temperature. It is relatively easy to suppress the first cell division by a 20- or 30-minute treatment of the eggs at 36°C, 4 to 5 hours after insemination at 20°. However, at the proper time of the second cleavage such eggs divide at once into four cells showing that the first division of the nucleus had not been suppressed. This can be demonstrated later by the chromosome counts in the resulting larvae, which are always diploid.

Theoretically, doubling of the chromosome number should also be obtainable by appropriate treatments with colchicine solutions. Keppel and Dawson (1939) showed that solutions of sufficient strength to retard or arrest mitosis in eggs of *Rana pipiens* also cause serious abnormalities in development, which does not proceed beyond the neurula stage. Sections of young abnormal embryos show groups of larger, presumably tetraploid, cells, as well as various irregularities of mitosis. Unpublished experiments of Rita C. Watson with eggs of *Triturus viridescens* demonstrated that these react in a similar way. Treatments with weaker solutions (1:5000 or less) had no effect and produced diploid larvae; with stronger solutions (1:1000) abnormal, inviable embryos resulted. In spite of these discouraging reports, more extensive experiments with colchicine and other mitotic "poisons" might still produce the desired results.

The effects of very strong (1%) colchicine solutions on mitosis in the tailfin of newt larvae were investigated by Barber and Callan (1943). Mitosis is arrested at metaphase, and the chromosomes assume various abnormal arrangements. A single, tetraploid resting nucleus may be produced, but recovery of the cells is much slower than after cold treatment because of the slow elimination of the poison, and the larvae rarely survive. In the survivors cell divisions are rare; a single tetraploid cell was seen five days after the end of the treatment.

(d) Experimental "allo-polyploidy" in *Triturus*

Experiments combining hybridization with induction of triploidy by subsequent cold treatment have been reported briefly by Costello (1942). Eggs of *Triturus rivularis*, fertilized by spermatozoa of *T. torosus* and cold treated should produce triploid embryos with two sets of *rivularis* and one set of *torosus* chromosomes. Costello merely states that "no larvae with accentuated maternal characteristics were obtained." Experiments of this type involving various combinations of species should produce interesting results, particularly if it should be possible to induce a doubling of the chromosome number in the zygote and to obtain tetraploid species hybrids.

(e) Polyploid larvae obtained as by-products in other experiments with amphibian eggs

Both Parmenter and Kawamura reported the occurrence of various heteroploid chromosome types among parthenogenetic larvae of frogs, in addition to the haploid and diploid individuals discussed previously. Parmenter (1933) listed a total of 29 embryos and larvae of *Rana pipiens* and *Rana palustris*, of which 12 were haploid, 10 diploid, 4 haploid/diploid mosaics, one diploid/triploid, one diploid/triploid/tetraploid, and one completely triploid. He suggested that the triploid condition resulted from the combination of a retained second polar body with a diploid group which originated through a doubling of the haploid set of the egg nucleus. In experiments with eggs of *Rana fusca*, Parmenter (1940) found 3 haploids, 4 haploid/diploid, one diploid, and 3 diploid/triploid larvae.

Kawamura (1939a), using eggs of *Rana nigromaculata*, obtained the following impressive series of chromosome types among his 413 parthenogenetic larvae: 202 haploids, 86 diploids, 95 triploids, 4 tetraploids, 12 hexaploids, 1 hyperdiploid (2N + 3), and several mosaics (8 haploid/diploids, 3 haploid /triploids, 1 haploid /pentaploid, and 1 triploid/hexaploid). Kawamura discusses in detail the possible modes of origin of the various types. The high frequency of triploids remains unexplained beyond the suggestion that they may have developed from eggs in which (1) the first polar body was retained, (2) two separate second maturation spindles were formed, of which (3) one only was located at the egg surface and produced a second polar body. This would leave three haploid sets of chromosomes in the egg. Such an origin of triploidy was actually described by Hiraiwa and Kawamura (1936) in parthenogenetic eggs of the worm, *Urechis*.

In experiments on androgenesis with eggs of *Triturus pyrrhogaster* Kaylor (1940a) obtained two triploid larvae. The available evidence does not demonstrate beyond doubt that these actually developed androgenetically, i. e., with three paternal chromosome sets, rather than from eggs in which the operative removal of the maternal chromosomes had not been successful.

(f) Experimental heteroploidy in other animals

Experimental induction of heteroploidy has been attempted with relatively few species of animals other than amphibians. The most extensive and successful experiments are those with eggs of the silkmoth, *Bombyx*. Many of the other investigations are incomplete or preliminary in nature. A brief review of the methods used and of the general results obtained follows.

Cold. The brine shrimp, *Artemia salina*, oc-

curs in bisexual and parthenogenetic races. Among the latter, diploid, tetraploid, and octoploid lines are found in different localities; eggs developing parthenogenetically give off a single polar body and retain the chromosome complement of the mother. Refrigeration of parthenogenetic eggs of a diploid race during the single maturation division prevented in some cases the formation of the polar body, so that tetraploid animals may be obtained by this method (Gross, 1932, 1935).

The experiments of Pincus and Shapiro (1939) on the effects of cold on unfertilized rabbit eggs should also be mentioned in this connection. A treatment at +6°C for 10 to 30 minutes may activate eggs in vitro or in the Fallopian tubes. One living young, a female, was obtained from experiments with sixteen rabbits in which probably over 200 eggs had come under the influence of the low temperature. The single female produced apparently was normal and therefore diploid, as might be expected if the cold in this case not only activated the egg but also suppressed the second maturation division.

Heat. Short heat treatments of eggs of the silkmoth (Hasimoto, 1933; Astaurov, 1940) have a double effect: they induce parthenogenesis as well as retention of the diploid chromosome number, since a single, equational maturation division takes place. Furthermore, in over 25 per cent of the heat-treated eggs, there is a tendency for the diploid cleavage nuclei to fuse after the first or a later cleavage mitosis, producing tetraploid or partly tetraploid females. Tetraploid eggs of such females may again be heat-activated and thus give rise to another generation of tetraploid females.

Colchicine. The attempts to induce polyploidy in eggs of various species of animals with colchicine solutions have been rather disappointing so far. The best results were obtained with eggs of the silkmoth which were treated within 2½ hours after laying with 0.05 to 0.4 per cent colchicine and produced "many polyploid individuals" (Hirobe, 1939). The ovaries of the polyploid females, however, were found to contain both polyploid (presumably tetraploid) and diploid cells.

Treatment of females of the wasp, *Habrobracon*, with 0.05 per cent colchicine induced the formation of many tetraploid oogonia in the ovaries. Some of the eggs examined after laying also contained the tetraploid chromosome number (Inaba, 1939, 1940).

Pincus and Waddington (1939) also observed tetraploidy in a number of rabbit eggs after treatments with various mitosis-inhibiting agents, including colchicine and heat; these eggs, however, usually failed to cleave during 24 hours of culture.

Extensive cytological observations on eggs of the fresh-water annelid, *Tubifex*, treated with colchicine showed that the maturation divisions are not inhibited even by strong solutions (1:500). There seems to exist a particularly sensitive period during the interphase following the first cleavage mitosis when the same and lower concentrations cause a complete disappearance of the mitotic apparatus and a dissolution of the nuclei. Concentrations of 1:10,000 to 1:20,000 induce atypical cleavage; with 1:30,000, development is normal. Although mitotic figures with an increased number of chromosomes have been observed in abnormally cleaving eggs, there is no direct proof that these cells are polyploid. The normally developing eggs apparently are all diploid (Lehmann and Woker, 1940; Woker, 1943, 1944).

Treatment of larvae of *Drosophila* produces polyploid areas in brain tissue (Braungart and Ott, 1942), and injection of 0.05 cc. of a 0.05 per cent solution into the body cavity of male grasshoppers may suppress the division of spermatogonia and spermatocytes; the latter may differentiate directly into polyploid spermatids and transform into giant sperm cells with one or more tail filaments (Dooley, 1941).

As a whole the observations seem to show that eggs during early cleavage are so injured by colchicine solutions in concentrations sufficient to affect mitosis that normal development does not take place. Further investigations on the production of diploid or polyploid eggs or spermatozoa by treatment of immature or mature individuals appear to be more promising.

Centrifuging. When eggs of the silkmoth are centrifuged for ten minutes, at 3500 revolutions per minute, from one to three hours after laying (i. e., during the maturation divisions), a considerable proportion of the resulting caterpillars are polyploid. Among 17,193 caterpillars Kawaguchi (1936) found over 13 per cent triploids, over 2 per cent tetraploids, and a single hexaploid individual. More hexaploid caterpillars were obtained by treating eggs deposited by tetraploid mothers.

Hybridization. The earliest experiments which produced polyploid animals were those of Standfuss, Federley, Harrison, and Meisenheimer (bibliography in Goldschmidt, 1931; and Coc-

kayne, 1938), in which F1 males from crosses between several species of moths were mated with females of one of the parent species. Because of the general failure of pairing between the two chromosome sets in the spermatocytes of the F1 males, diploid or nearly diploid spermatozoa are produced which, in fertilizing haploid eggs, give rise to triploid or sub-triploid individuals.

4. Primary effects of changes in number of chromosome sets: changes in nuclear and cell size

The immediate effect produced by a change in chromosome number is a corresponding change in the size of the nuclei and the cells. Because of the constancy of this relationship the alteration in nuclear and cell size can in turn be used as a valuable criterion for the identification of heteroploid individuals (cf. Figs. 1 and 4; Table 2). The measurements on nuclei of heteroploid salamander larvae were made largely for diagnostic purposes and not for an accurate determination of the amount of increase in nuclear volume caused by the addition of each successive chromosome set. The great range of variability between individual nuclei, and between samples of nuclei from different individuals having the same number of chromosomes, would call for very large series of measurements. Also, no attempt has been made so far to determine accurately the changes in the size of the cells, since their boundaries are usually not clearly marked. Although it is evident that the cell size increases with the nuclear size, it is not possible to state whether or not the nucleoplasmic ratio remains constant at all levels of polyploidy.

More or less accurate determinations of the volume of the nuclei in triploid, diploid, and haploid amphibian larvae have been made by several investigators. In these calculations, the nuclei are usually treated as spherical or nearly spherical, and the ratio of the volumes is obtained by comparing the cubes of the radii. The diploid/triploid ratio was generally found to be close to 1:1.5 in nervous tissue, cartilage, and muscle cells (G. and P. Hertwig, 1920, *Rana esculenta*; Kawamura, 1939a, *Rana nigromaculata*). Böök (1944) gives the same ratio for spermatocytes in adult *Triton taeniatus*, while for nerve, cartilage, and muscle cells of larvae he finds a ratio varying between 1:1.63 and 1:1.74.

The haploid/diploid ratio is usually near the expected 0.5:1.0 value (O., G., P. Hertwig, 1913 to 1920). In cartilage nuclei of *Triton taeniatus*, G. Hertwig (1927) found a ratio of 0.31:1.00, but a higher value of 0.60:1.00 is given by both O. Hertwig (1913) and Böök (1941) for nuclei of the medulla in larvae of the same species.

Comparison with invertebrates

In spontaneous and experimentally induced polyploid invertebrates the nuclei are generally larger (*Drosophila*, *Bombyx*). In the latter, eggs of tetraploid females have roughly one and one-half times the volume of those of diploid individuals (Astaurov, 1940) Kawaguchi (1936) mentions that the eggs of hexaploid females are still larger and gives the following ratios for cross-sectional areas of nuclei of primary spermatocytes: diploid/triploid/tetraploid = 1.0/1.4/1.9. This shows that the volumes of the nuclei increase more than in direct proportion to the chromosome number, since with direct proportionality of the volumes the areas of the cross sections should be as 1.00/1.31/1.58, if the nuclei are spheres. The cells of triploid silk glands are also larger than expected.

In those species of invertebrates in which permanently polyploid, parthenogenetic races occur, the nuclei and cells are also generally larger than in corresponding tissues of diploid animals, e. g., in the triploid race of the crustacean, *Trichoniscus* (Vandel, 1928), and in the tetraploid and octoploid races of the brine shrimp, *Artemia salina* (Artom, 1925). In *Artemia*, the tetraploid/diploid ratio varies between different tissues (Artom, 1923). Recently Barigozzi (1941) described very large differences between individual females of an octoploid race in the average size of the nuclei of the gut epithelium. Major deviations from the average tend to be the same in mother and offspring, indicating the influence of genetic factors; however, it is certain that even the extreme deviations are not connected with any change in chromosome number. It is not known whether changes in the size of the chromosomes or differences in specific genes affecting nuclear and cell size are involved. In the bagworm moth, *Solenobia*, Seiler (1936) found the unusual situation that eggs of tetraploid females are of the same size as those of diploid females but are twice as numerous. The somatic cells are apparently larger in the tetraploid individuals, as is shown by their larger body size.

The relation of cell size to chromosome number is of particular interest in the Hymenoptera, where the males are normally haploid and parthenogene-

tic, while the females are diploid and develop from fertilized eggs. Male bees did not show consistently smaller nuclei in the many tissues studied by Oehninger (1913). In the parasitic wasp, *Habrobracon*, Speicher (1935) found an increase of about 5 to 16 per cent in the average area of the wing cells of diploid females as compared with haploid males; however, in diploid, biparental males, which occur occasionally, the wing cells were about 28 per cent larger than in diploid females, and in triploid females the increase over diploid females was about 86 per cent. The latter figure may not be reliable, since the triploid females differed from the diploid by a gene affecting the structure of the wings. Similar observations have been made on the size of the facets of the eye, which are produced individually through the secretory activity of two cells (Speicher and Speicher, 1940; Risman, 1942).

Altogether these observations indicate that in the normal, haploid males the size of the cells has been readjusted to nearly normal dimensions through some process of regulation, possibly through a slow selection of genes increasing the cell size. In exceptional diploid males and in their triploid daughters, on the other hand, no regulatory mechanism of this type could be developed, since they occur sporadically and are not exposed continually to the action of selection.

It should not be forgotten, furthermore, that in the Hymenoptera the study of the cell size/chromosome number relationship is complicated by the fact that certain tissues of normal haploid males and diploid females regularly become polyploid to a variable degree during development, as is the case in many other insects (Dodds, 1938, on gallwasps).

Comparison with plants

Studies on the relation of cell size to chromosome number in plants have demonstrated a striking difference between the experimentally induced and occasional, spontaneous polyploids in normally diploid species, on the one hand, and the naturally occurring polyploid races and species on the other. In the latter, there is no consistent relation between chromosome number and cell size (cf. Darlington, 1937). Of 48 naturally tetraploid races investigated, only 14 possessed larger cells (Müntzing, 1936). In induced polyploids there is a close proportionality between cell size and chromosome number. In *Nicotiana*, for instance, the cells increase throughout the plant with the addition of each chromosome set, from the haploid to the octoploid condition (H. H. Smith, 1943). As in animals, the polyploid/diploid ratio may vary between different tissues. In the periwinkle, *Vinca rosea*, the guard cells of the stomata are much larger in tetraploid leaves and can be used to identify polyploid individuals, as in other plants. The ordinary epidermal cells, however, are of about the same size as in diploid leaves (Cross and Johnson, 1941). In maize, the nuclei and cells of the shoot apex are almost exactly twice as large in tetraploid seedlings as in diploid ones. In the mature leaf, the average size of the tetraploid cells is only 1.6 times the diploid size; furthermore, the variability in different tissues and in the same tissue in different regions is very great (Randolph, Abbe, and Einset, 1944).

The nucleoplasmic ratio (or cytonuclear ratio, cf. Sinnott and Trombetta, 1936; Trombetta, 1942) may not remain constant with higher degrees of polyploidy. In *Crepis capillaris* the ratio of the volumes of the nuclei in meristem cells of the root of a diploid, a triploid, and a pentaploid plant was 1:1.9:4.1, the ratio of the cell volumes 1:1.3:2.5 (Navashin, 1925). Endosperm cells of tetraploid maize show an opposite trend. In diploid plants these cells are regularly triploid, since their nuclei are derived from a process of fusion between three haploid nuclei at the time of fertilization; in tetraploid plants, the endosperm is therefore hexaploid. While their cell volume is 3.5 times the normal, the volume of their nuclei has increased only 2.5 times (Randolph and Hand, 1938, 1940).

The whole problem of the relation of cell size to polyploidy offers special aspects in plants because of the secondary enlargement or expansion of the cells connected with extensive vacuolization. In early fruit primordia of cucurbits the cells are twice as large in tetraploid plants as in the diploid; after cell divisions cease, however, the diploid cells expand more and, at maturity, reach nearly the same size as the tetraploid (Sinnott and Franklin, 1943).

Signi cant additions to the study of the factors affecting cell size have been made by investigations on mosses, which are normally haploid (cf. Wettstein, 1927). Measurements have shown the existence of specific differences in the increase of cell volume following experimental chromosome doubling. The haploid/diploid ratio may vary from 1:1.45 to 1:3.94 in different species. Recently, Barthelmess (1941) studied nine races of *Physcomitrium piriforme* which differ considerably in the size and shape of the cells in their normal,

haploid condition. When diploidy is induced experimentally, the cell volume increases in some races from 1 to 1.64, in other races it actually decreases from 1 to 0.9. Of the greatest theoretical importance are Wettstein's (1937) observations on an experimentally induced diploid clone of *Bryum caespiticium* in which the cell size at first was 37,800 cubic micra, as compared with 16,900 cubic micra in the original haploid plant. In the course of eleven years, however, the cell size was reduced slowly, until it reached the value of 18,600 cubic micra. In a naturally occurring diploid clone of the same species, the cell size was found to be 21,900 cubic micra.

Changes in the shape of cells

Changes in chromosome number may alter different dimensions of the cells to a different degree and thus produce a change in their shape. In tetraploid plants of *Vinca rosea* the cells of the apical meristem are broader but not higher; the lateral dimensions are increased by one-half to two-thirds, while the vertical dimensions may be slightly reduced (Cross and Johnson, 1941). The nine races of the moss *Physcomitrium* studied by Barthelmess (1941) varied not only in cell size but also in cell shape. Chromosome doubling produced a broadening of the cell in races with narrow cells in the normal, haploid condition; in races with short haploid cells, diploidy caused the cells to become longer and narrower.

Changes in the shape of the nuclei may also be associated with heteroploidy in salamander larvae. The nuclei of haploid erythrocytes are relatively shorter and more rounded than those of diploid cells, and the nuclei of haploid connective tissue cells also tend to be less irregular in shape. A decrease in the length/breadth index of the nuclei of haploid erythrocytes and kidney cells has also been described by Böök (1941). This might be a simple consequence of the different surface properties of the smaller haploid nuclei. Changes in the shape of cells are conspicuous in organs where they are arranged in thin layers, as in the epidermis or in the kidney tubules. This is a point of considerable theoretical importance, to be discussed in a later section.

5. Secondary effects of changes in chromosome number

Most of the macroscopic effects of heteroploidy, both morphological and physiological, may be termed secondary, since they appear to be consequences of the changes in nuclear and cell size which are the primary results of alterations in chromosome number. It must be emphasized, however, that frequently it will not be easy to determine whether the ultimate cause of a visible effect is to be found solely in the change in the total mass of chromosome material affecting the size of the nuclei and cells, or, partly or entirely, in the change in the dosage of genes, which may influence the expression of certain individual genes while that of others remains the same. The latter case would represent a second type of primary effect of heteroploidy (see p. 121).

On the other hand, it might be possible to classify some of the effects described in the following pages as still more remote links in the chain of reactions set up by the initial change in chromosome number, i. e., as direct or even indirect consequences of some secondary effect. Until we know a great deal more about the causation of some of the expressions of heteroploidy in amphibian development it will suffice to keep these various possibilities of interpretation in mind for a future reconsideration of the facts.

In view of the close interrelations between all the processes of development, it may be misleading to treat them separately in the discussion. For the sake of clarity, however, it would seem advantageous to group the facts under the following headings which will help us to focus our attention consecutively on the various problems that are involved.

(a) Body size, organ size, and their relation to cell size and cell number

Haploidy. All investigators agree that haploid amphibian larvae are smaller than normal to a varying degree (Fig. 7). The earliest detailed observations by O. Hertwig on *Triton taeniatus* indicated a reduction in body length and in the size of many organs to three-fourths or two-thirds of the normal measurements. Recently, Böök (1941) described a similar reduction in the size of a larva of the same species, and estimated that the volume of the central nervous system was about 61 per cent of the normal. In anurans, G. Hertwig (1913) found twice the normal cell number in haploid gastrulae but a reduction in later stages of development, so that the individual organs were only half normal size, with the exception of the ear vesicles, which were as large as in diploid larvae. Porter (1939) mentions that in haploid tadpoles of *Rana*

pipiens the notochord has the same cross sectional area as in the diploid while the other organs are clearly reduced. Such exceptional reactions of single organs have considerable interest for the study of the factors controlling growth and organ size and should be investigated more closely.

The relation of size and cell number was studied in lenses developed from haploid epidermis which had been transplanted to the eye region of diploid embryos (Rotman '40). At the time of separation from the epidermis, the lens had the same size as the diploid on the unoperated side and contained about 69 per cent more cells per unit volume. A similar relation was found in a completely haploid control embryo; this would indicate that an adjustment in cell number compensating for the decrease in cell size may take place very early in development of an organ, although in the case of the lens this regulation may be largely dependent on the size of the optic cup inducing its formation in the overlying epidermis.

The fact that the haploid larvae which appeared spontaneously in several species of salamanders in our own laboratory were also more or less dwarfed demonstrates clearly that the various treatments which are used to induce haploidy experimentally are not responsible for this effect (Fig. 7: 1–2). The size of individual haploid larvae varies considerably, however, and in at least one case, a larva developed from a refrigerated egg of *Triturus pyrrhogaster*, was almost normal (Fig. 7: 4).

A detailed investigation was made of the microscopical anatomy of the oldest haploid salamander obtained so far which died at the conclusion of metamorphosis (Baltzer, 1922; Fankhauser, 1938a). The animal was dwarfed (cf. Fankhauser, 1937a, Fig. 6) but more than half normal size. Correspondingly, most of the organs were larger than half size, with more numerous cells than the diploid organs, with the exception of the cartilages of the larynx, which showed the same cell number in cross section and were almost exactly half size. On the other hand, some glands attained normal size, either through enlargement of the individual structural units, such as the tubules of the lacrymal glands, or through an increase in the number of the units which remained small themselves, as in the case of the follicles of the thyroid.

It must be mentioned that this haploid developed from an egg fragment, which included considerably more than half of the mass of the egg. The initial mass of cytoplasm and yolk has been shown to be of little importance, however, since diploid larvae from egg fragments or isolated blastomeres of the two-cell stage, although half-size at first, reach approximately normal size at the time of metamorphosis (Spemann and Falkenberg, 1919, *Triton taeniatus*; also unpublished observations on *Triturus viridescens*).

Triploidy. Triploid salamander larvae, as a rule, are not noticeably larger than the diploid. In *Triturus viridescens* the size range of triploids is approximately normal (Fig. 5); a single larva among the many which have been raised to metamorphosis so far was considerably larger (Fankhauser, 1938c). The influence of differences in the amount and kind of food given to the larvae can be eliminated by maximal feeding with *Daphnia*, which may be accomplished by having *Daphnia* present in the culture dishes at all times, or, still better, by raising the larvae in large *Daphnia* cultures. The latter method produced particularly vigorous animals, but again, diploid and triploid larvae responded in the same way. In *Triturus pyrrhogaster*, observations on a smaller number of animals showed that maximal feeding may bring out a slightly greater response in triploids (Fankhauser, Crotta, and Perrot, 1942). Triploid *Eurycea* larvae may or may not become slightly larger than the controls; in some cases they are even smaller (Fankhauser, 1939; Michalski, 1942). In axolotls, which can be easily raised to sexual maturity in the laboratory, it will be possible to settle the question of the final size reached by adult triploids. So far, observations on numerous larvae have shown that in some spawnings the triploids are uniformly large and vigorous, while in others they are lagging behind the controls.

In triploid *Triturus viridescens* the normal size of the organs at the time of metamorphosis is caused by a decrease in the number of cells that neutralizes the increase in cell size (Fankhauser, 1941a); the notochord alone may be an exception, since it appears larger in cross-section. The gonads present a special case, since their development is influenced by the disturbance of the sex chromosome mechanism and will be discussed later.

In general, the observations on triploid amphibian larvae made in other laboratories are in agreement with our findings. Bŏŏk (1944) reports that triploid larvae of *Triton taeniatus* are normal in size and have fewer cells in all the organs studied. The only adult triploid salamander found so far was large but within the normal size range of

diploid animals (Böök, 1940). On the other hand, Parmenter (1933) noted that a triploid parthenogenetic tadpole of *Rana pipiens* was conspicuously large. The observations of Kawamura (1939a) on numerous triploid parthenogenetic larvae of *Rana nigromaculata* are difficult to evaluate because of the high proportion of abnormal individuals present. His drawings show a similar range of body size in triploid and diploid tadpoles although the former seem to be somewhat smaller on the average.

Higher degrees of polyploidy. Of the few tetraploid larvae seen so far, the first two, found in *Eurycea bislineata*, were slightly smaller than the controls from the beginning of the observations. The single tetraploid larva of *Triturus viridescens* was smaller at hatching but finally reached approximately normal size at metamorphosis, although with considerable delay (Fig. 5: 7).

All of the eight pentaploid larvae of *Triturus viridescens* seen so far were approximately normal in size at the time of hatching (Fig. 6: 1–2; cf. Fankhauser, 1940). The three which were raised to metamorphosis were greatly retarded in development but metamorphosed at about normal size (Fig. 6: 5). This was also true of a single pentaploid larva of *Triturus pyrrhogaster* which was discovered last spring (Fig. 6: 6–8). Two pentaploid axolotl larvae likewise remained behind the diploid in size as long as they lived.

Tetraploid and hexaploid individuals were found by Kawamura (1939a) among his parthenogenetic frog tadpoles The size of the young larvae was within the diploid range as far as can be told from the illustrations; none of the animals were raised to a more advanced stage.

Cursory examination of sections through tetraploid and pentaploid salamanders shows at once that throughout the body the larger size of the cells is met by a decrease in cell number. As far as the observations go we may conclude, therefore, that the body size of polyploid amphibian larvae at comparable stages of development is always the same, irrespective of the chromosome number and the cell size, since the latter is compensated by a corresponding reduction in the number of cells. Haploid larvae as a rule are smaller but show at least a partial compensation in cell number (cf. Sharp, 1943, Fig. 157).

Comparison with invertebrates. The classical studies of Boveri (1905) on eggs of sea urchins, which first demonstrated a constant relationship between chromosome number, nuclear and cell size in animals, also showed that the size of the young embryo at the end of cleavage is not affected. A haploid gastrula consists of smaller but more numerous cells, a tetraploid contains larger but fewer cells. At the early pluteus stage haploids are smaller (cf. Hoerstadius and Wolsky, 1936); no information on the later development of polyploid eggs seems to be available.

The relation of chromosome number to adult body size in various species of arthropods was discussed at length in a previous publication (Fankhauser, 1941a, pp. 166–7, Table 2). Gigantism was reported in tetraploid and octoploid brine shrimps, *Artemia*, although various statements indicate that this may not be the general rule in this species. Artom (1927, 1928, 1929) emphasizes the pronounced gigantism of embryonic stages, in which the total cell number seems to be normal, while in the adult tetraploid the "potential" gigantism may be masked by suboptimal environmental conditions. He also stresses the fact that the gigantism may be restricted to organs with constant cell number, as the central nervous system or the eyes; the same ganglion, for instance, is made up of from 115 to 130 cells in both diploid and tetraploid individuals. Octoploid Artemia are hardly larger when they reach sexual maturity, but seem to grow larger with age (Gross, 1932).

In the bagworm moth, *Solenobia*, pupae of the tetraploid race are twice as large as diploid pupae, while triploid pupae are intermediate though very variable (Seiler, 1927, 1936, 1937). Females of the triploid race of the isopod *Trichoniscus* are 4.5 mm. long on the average, diploid females average 3.3 mm. (Vandel, 1927, 1928). In *Drosophila melanogaster*, triploid females are characterized by large, stocky build, large, roughish eyes with large ommatidia, and by coarse bristles (Morgan, Bridges and Sturtevant, 1925). According to Dobzhansky (1941), they differ from the diploid in body proportions rather than in actual size. Triploid females of *Drosophila americana* are somewhat larger and stockier and have roughened eyes (Stalker, 1942).

Triploid and tetraploid silkworms are not larger than the diploid, according to Kawaguchi (1936) and Astaurov (1940), because the cell number is reduced in inverse proportion to the cell size, e. g., from 680 to 443 in triploid silk glands. In this species the reactions to changes in chromosome

number thus seem to be identical with those shown by amphibian larvae.

Comparison with plants. From the great mass of available data a few striking illustrations have been selected, from recent publications, to show the general trends. Long established polyploid races or species may or may not show gigantism, depending in many cases on whether or not the size of the individual cells has returned to normal (cf. Darlington, 1937). Spontaneous and induced tetraploids in diploid species are consideraby larger than diploids as a rule, while triploids are intermediate in size (cf. Müntzing, 1936). In *Nicotiana*, for instance, there is a general increase in the size of the plant from the haploid to the tetraploid condition (H. H. Smith, 1943), parallel to the increase in cell size. In corresponding cross sections of diploid, triploid, and tetraploid roots Warmke and Blakeslee (1939) found approximately the same total number of cells and the same number of cell layers (about six) in the cortex.

The increase in plant size may continue with the addition of a fifth and sixth set of chromosomes (e. g., in hexaploid *Cuthbertia*, Giles, 1942). Octoploid plants, however, are smaller than the diploid as a rule in spite of their large cells (*Nicotiana*, Greenleaf, 1938, H. H. Smith, 1943; *Cucumis*, Shifriss, 1942; *Galeopsis*, Müntzing, 1941; maize, Randolph, unpublished, cf. Greenleaf, 1938, p. 458).

The effects of haploidy may also differ in different species. In *Datura stramonium* and *D. Metel*, for instance, haploid plants are less vigorous and dwarfed, as is the general rule in other genera of plants. In *Datura pruinosa* they are nearly normal in size (Satina, Blakeslee and Avery, 1937).

The potential gigantism of polyploid plants may be greatly influenced by both environmental and hereditary factors. Tetraploid individuals of the cucumber, which are more vigorous when grown in the greenhouse, do not show *gigas* characters in the field (Shifriss, 1942). In maize, tetraploid plants in non-inbred strains show normal or increased vigor; in inbred strains they are much shorter and less vigorous than diploids (Randolph, 1942).

Of the greatest interest from our standpoint are recent developmental studies on polyploid plants which have shown that the embryo as a whole, or the rudiments of various organs, may show typical *gigas* characters which are modified or completely lost during later stages of development. According to Fabergé (1936), tetraploid embryos of the tomato are 30 per cent heavier than normal but lose this advantage during the first eleven days after sowing, so that the tetraploid plant may not differ significantly in the total amount of substance produced. In maize, the shoot apex of tetraploid seedlings shows "ideal" *gigas* characters, while the volume of the mature leaf is only 1.6 times the normal, although the total cell number is approximately the same as in a diploid leaf (Randolph, Abbe, and Einset, 1944). In squashes, the young tetraploid ovary is about twice as large as the diploid, but the mature fruit is normal in size because the expansion of the cells following the cessation of cell multiplication is much reduced (Sinnott and Franklin, 1943).

This last observation indicates that in plants, as well as in animals, the quantitative effects of the initial change in cell size may be cancelled completely, although this compensation is achieved here, not through a reciprocal change in cell number, but through a modification of the secondary expansion of the individual cells by vacuolization, a process which is of great importance in plants but absent in most animal tissues.

(b) Rate of development

Haploidy. The development of haploid amphibian embryos is significantly slower than that of the diploid (Fig. 7: 1, 2, 5; cf. the series of photographs in Fankhauser, 1937, Figs. 2 to 4). In most of the haploid eggs or egg fragments of various species of newts, cleavage is slower than in the controls; usually there is a pronounced delay already in the appearance of the first cleavage furrow (O. Hertwig, 1913, Spemann, 1914, Baltzer, 1920, *Triton taeniatus*; Fankhauser, 1925, 1934a–c, Hadorn, 1932, 1934, *Triton palmatus*; Kaylor, 1937, Fankhauser and Moore, 1941a, *Triturus viridescens*; Fankhauser, 1937a, Kaylor, 1940, *Triturus pyrrhogaster*). Bŏŏk (1941) alone reported an accelerated rate of cell divisions in a haploid egg of *Triton taeniatus*. In anurans, on the other hand, the cleavage of haploid eggs takes place at the normal rate, while later development, from the gastrula stage on, is retarded (Parmenter, 1933, Porter, 1939, *Rana pipiens*).

It would be important to know whether the rate of growth and the rate of differentiation are affected to different degrees by haploidy. That cell division, the basic process of growth, is slowed down in haploid cells is shown not only by the

lower rate of cleavage in haploid eggs of salamanders, but also by the lower rate of regeneration of the tailtip following amputation in the young larva (*Triturus viridescens*, *T. pyrrhogaster*), and by the behavior of haploid limb buds or differentiated limbs when transplanted to diploid embryos or larvae (G. Hertwig, 1927).

The retardation of the process of gastrulation, on the other hand, which in androgenetic eggs of *Triturus viridescens* may begin from six to nine hours later than in controls and take 32 instead of 24 hours (at 21°, Kaylor, 1937), indicates that the morphogenetic movements which are largely associated with changes in the shape and arrangement of cells (Holtfreter, 1943) are also affected. Retardation in the differentiation of various organs is mentioned specifically by P. Hertwig (1916, *Triton vulgaris*), while G. Hertwig (1913, *Bufo vulgaris*) stresses the delayed differentiation of the ear vesicles and liver, and Porter (1939, *Rana pipiens*) notes a similar retardation in the differentiation of the eye and gut.

The single haploid salamander that could be raised beyond the early larval stage showed pronounced retardation in later development, including the onset of metamorphosis (Baltzer, 1922). At the completion of metamorphosis, all the organs seemed to be essentially normal histologically and to have reached the same degree of differentiation as in a diploid animal in a corresponding final stage of transformation (Fankhauser, 1938a).

This problem should be analysed by the culture of haploid tissues in vitro where the detrimental influence of the generally lowered viability of the haploid organism as a whole may be eliminated. Observations on four explants from haploid gastrulae of *Triton alpestris* (Hadorn, 1934, pp. 722–724), which were made to compare their performance with that of tissues of haploid androgenetic hybrids, did not show any striking differences from diploid explants. In this connection recent observations on the growth rate in vitro of excised tomato roots are of interest, as showing that under the favorable conditions of the culture haploid roots may grow as well as diploid (Robbins and Kavanach, 1943). It must be pointed out, however, that haploid individuals of tomatoes and other species of plants may grow surprisingly well when compared with diploids. Lindstrom (1936, p. 208) mentions that both growth and regeneration (from cuttings or from callus) are faster in haploid plants than in diploid, a statement which would hardly seem to apply to plants in general.

Polyploidy. The general rate of development of triploid salamander eggs is entirely normal with regard to both growth and differentiation, as far as can be told from the appearance of the living embryos and larvae. In later stages of development the growth rate may remain the same as in the diploid or may increase slightly (*Triturus viridescens*, *Triturus pyrrhogaster*, *Eurycea bislineata*). Among axolotl larvae, the growth rate is about the same in triploids as in diploids; in one spawning, the triploid larvae seemed to lag in growth (unpublished observations of R. R. Humphrey).

The rate of regeneration of the tail and limbs was carefully studied in triploid and diploid larvae of *Triturus viridescens* at various stages of development, but no significant difference could be detected between the two groups of animals (unpublished experiments of Rita C. Watson). This indicates that the rate of division must be normal or nearly normal in triploid cells.

Triploidy often causes a delay in the onset of metamorphosis (Fig. 5: 5–6). The duration of the larval period varies considerably between diploid individuals within a group of common ancestry, raised at the same time, and still more between different groups derived from different matings. These group differences may be partly hereditary, partly caused by differences in diet, since the groups raised on a pure *Daphnia* diet metamorphosed earlier than those which were fed mostly *Tubifex* or *Enchytraeus* worms.

Metamorphosis is most conveniently timed by using the day of the first molt, since the preceding "premetamorphic" changes, like the reduction of the tailfin and gills and the changes in the pigment pattern, are slow and gradual. Between several groups of diploid animals raised during the past four years the average age at the first molt varied from 77 to 115 days, the mean for all 69 animals being 89.4 days. In the corresponding groups of triploids, including a total of 32 animals, the range was from 84 to 145 days, and the mean 102 days.

The few tetraploid salamander larvae that have come under observation so far all developed considerably more slowly than the diploid. The most complete records available are those for the single tetraploid larva of *Triturus viridescens* which, from an early larval stage on, was several days behind in differentiation and growth. Regenera-

BOSTON UNIVERSITY
COLLEGE OF LIBERAL ARTS
LIBRARY

tion of the amputated tailtip also was slower than in the diploid. When the diploid larvae entered metamorphosis at the age of eleven to twelve weeks, the body length of the tetraploid was only about three-fourths of the normal. However, this animal remained in the larval stage several weeks longer, growing steadily to approximately normal size when it molted for the first time at the age of nineteen weeks (Fig. 5: 7).

A total of eight pentaploid larvae of *Triturus viridescens* have come under observation so far. The embryonic and larval development, up to almost complete differentiation of the forelimbs, proceeded at a normal rate in the seven animals for which sufficient records are available. Five larvae were preserved at the time of the first appearance of the hindlimb buds, while the remaining three were raised to metamorphosis. Two of the latter remained behind in differentiation, to varying degrees, during the development of the hindlimbs; one proceeded with differentiation at the normal rate to almost complete formation of the toes. In all three, however, the rate of growth was greatly reduced from the time of the appearance of the hindlimb buds on, though again not uniformly. As in the case of the single tetraploid, the animals remained longer in the larval stage than the controls. Two underwent the first molt about three and five weeks, respectively, later than the average diploid; by this time one had reached a size typical for diploid animals at metamorphosis; the other was still considerably smaller (Fig. 6: 4–5). The third pentaploid belatedly showed the typical changes in pigmentation and reduction of the gills and tailfin but died without having molted, eight weeks after the first molt of the average diploid, still strikingly dwarfed when compared with diploids at this stage of transformation (Fig. 6: 3).

The single pentaploid larva of *Triturus pyrrhogaster* found so far also showed a differential effect of the high chromosome number on the rate of growth and differentiation. The latter was delayed slightly during later stages of the development of the hindlimbs, while the growth rate was greatly reduced (Fig. 6: 6). The larval period was again prolonged, so that the animal metamorphosed at a size approximately typical for the species, almost eight weeks later than the diploid controls (Fig. 6: 7–8).

The various metamorphic changes were normal in the pentaploids, as far as could be determined from their external appearance. This does not preclude the possibility that a close study of the sections may reveal some differences in the histological response of various organs. The appearance of the thyroid will be particularly interesting, although it will not decide the question whether the delay in metamorphosis was caused originally by a slower differentiation of this gland and a delayed release of the secretion, or by a tardy response of the reacting tissues to the thyroid hormone.

The slow growth rate of the pentaploids during later larval development may be caused in part by the generally lower food intake of these animals. There are evidences, however, that this is not the only and perhaps not the most important factor. On the one hand, one pentaploid larva, which during most of the larval period took almost as much food as the controls, remained much behind in growth, although not as much as another pentaploid of exactly the same age which fed less. On the other hand, regeneration of the amputated tailtip in the young larvae which had not yet reached the feeding stage proceeded considerably more slowly in the pentaploids. This fact indicates an inherently lower growth rate of pentaploid tissues, since it is well known that sub-optimal feeding, or even starvation, has little influence on the rate of regeneration in older diploid larvae. Experiments on tail and limb regeneration in older pentaploid animals have not yet been carried out.

Comparison with polyploid invertebrates and plants. The available information on the rate of development of polyploid invertebrates is rather incomplete. In the moth *Solenobia*, tetraploid individuals develop more slowly than diploid, while triploids show an intermediate rate (Seiler, 1927). In triploid and tetraploid silkworms the rate of mitosis is decreased apparently in inverse proportion to the increase in chromosome number and cell size (Astaurov, 1940); in eggs containing diploid as well as tetraploid and octoploid cleavage nuclei, the lower mitotic rate of the polyploid nuclei is obvious (Frolowa, 1940). In the brine shrimp *Artemia*, the rate of division of polyploid nuclei is also lower at later stages of development; however, tetraploid embryos grow more rapidly at first and show a precocious differentiation of the organs, particularly of the optic ganglia and the eyes (Artom, 1927).

The observations on the rate of development of polyploid animals are in general agreement with those on plants. The growth of some triploid plants, e.g., *Crepis*, pine-apple, apple, is slower than

that of the diploid (cf. Müntzing, 1936); in others it is more rapid, e. g., *Populus tremula* (Nilsson-Ehle, 1936). In experimentally induced tetraploid plants, the time from planting of the seed to beginning of flowering is increased (Kostoff, 1938). In *Nicotiana Sanderae* and *N. Langsdorffii* maturity is delayed more and more with the addition of each set of chromosomes (H. H. Smith, 1943). Tetraploid plants as a rule are slow growing; in octoploids, the rate of growth is reduced still further, e. g., *Nicotiana* (Greenleaf, 1938). In cultures of excised tomato roots, the tetraploids also show a much reduced growth; the dry weight of the tissue produced during a certain period is only one-third to one-half of that of diploid cultures (Robbins and Kavanach, 1943). In those cases where the rate of cell division was studied directly it was found to be reduced in tetraploids (tomato, Lesley and Lesley, 1930; maize, Randolph, Abbe and Einset, 1944; see also Eigsti, 1942).

The first comparison of the growth hormone content of diploid and related tetraploid plants, at the same stage of development and tested on the same day, has just been published by Gustafson (1944). He found that tetraploids of two varieties of marigolds had 58.1 per cent and 76.3 per cent as much hormone, respectively, as the diploids, and tetraploid cherry tomatoes 56.8 per cent as much as the diploids. The general appearance of the young tetraploid plants gave no indication of the lower hormone content; however, they blossomed considerably later than the diploids.

(c) Physiological effects

Haploidy. All investigators agree that the viability of haploid amphibian embryos and larvae is greatly reduced. The rate of mortality at various stages of embryonic and larval development is high; of the several thousand haploid larvae observed by the Hertwigs over a period of years none developed beyond the first larval period (P. Hertwig, 1923). In spite of numerous attempts to raise haploids, Baltzer's (1922) *Triton taeniatus* remains the only haploid to have reached metamorphosis.

The effects of haploidy are not equally severe in different taxonomic groups of amphibians. P. Hertwig (1923) mentions that haploid newt embryos are more normal than those of toads, and these in turn are less affected than frog embryos. Similar differences seem to exist between species of newts, since haploid larvae of *Triturus pyrrhogaster* are more normal as a whole than those of *Triturus viridescens* (Fankhauser, 1937a; Kaylor, 1940a).

The actual causes of the poor viability of haploid embryos are still not well understood (cf. Fankhauser, 1937a, pp. 12–14). The various hypotheses which have been suggested may be briefly summarized under the following headings:

(1) Delayed, harmful effect of the treatment used to induce haploidy. A latent toxic effect on the egg may be associated with radiation of one of the gametes, or with treatment of the sperm with trypaflavine (Dalcq and Simon, 1931). However, it is unlikely that simple operative techniques like the removal of a small amount of egg material with the second maturation spindle should have a deleterious effect. Furthermore, it should be emphasized here that the haploid embryos which have appeared spontaneously in several species of salamanders are not more normal than those produced experimentally.

(2) Edema. The great majority of haploid amphibian larvae sooner or later develop generalized edema, which may be severe enough to cause their death (Dalcq, 1932). A malfunction of the excretory system is the most widely accepted cause of this condition in haploids, although no concerted effort has been made to rule out other possibilities, such as deficiencies of the circulatory system or, perhaps, a general change in the water relations of haploid cells. An interesting approach to the study of this problem was made by Kaylor (1940b), who united haploid with diploid embryos in parabiosis. One of these pairs survived long enough to show the gradual regression of an early edema in the haploid partner when sufficient connection had been established with the circulation of the diploid. The disappearance of the edema, however, did not improve the further development of the haploid member.

In several experiments haploid newt larvae were obtained which were free from edema (*Triton taeniatus*, G. Hertwig, 1927; *Triturus pyrrhogaster*, Fig. 7: 4). Such larvae develop well until the supply of yolk is exhausted. After this they usually cannot be induced to feed, or, in a few cases, begin to take small *Daphnia* but lose their interest in food again after a short while. In such non-edematous animals the factor limiting their life span may well be their generally low reactivity or, perhaps, some more specific sensory disturbance.

(3) Abnormal utilization of yolk supply. The observations of the rate of utilization of the yolk in various organs of haploid embryos are conflicting and have led to the formulation of two diametrically opposed hypotheses. G. Hertwig (1913) found a lower rate of yolk consumption in haploid embryos of anurans and suggested that these embryos die because the slowly growing haploid cells are unable to take care of the normal yolk supply of the egg. Tchou-Su (1931), on the other hand, claimed that the yolk granules disappear more rapidly from the intestinal and germ cells of haploid toad embryos, which thus actually "die from their excessive oxidations." Since haploid embryos have smaller but more numerous cells, the total surface of the nuclei, i. e., the total zone of interaction between nuclei and cytoplasm, would be greater and the rate of metabolism thus increased. Recently, Porter (1939) again noted that in androgenetic embryos of *Rana pipiens* the yolk granules disappear more slowly from various organs than in the controls.

(4) Expression of recessive lethal factors in haploids. A highly suggestive genetical explanation of the poor viability of haploid amphibian larvae was proposed by Darlington (1937) and others. Recessive lethal factors in single dose appear to be widespread in natural populations. When isolated from the normal dominant allele in haploid embryos, they can produce their effect and kill the embryos at various stages of development. This hypothesis does not explain the normal viability of diploid parthogenetic frogs (Parmenter, 1933) and grasshoppers (King and Slifer, 1934), if their diploid condition was produced by doubling of the haploid chromosome set during the first or a later cleavage mitosis, a process which would result in a completely homozygous condition. In other cases diploidy may be the result of the retention of two sets of maternal chromosomes through suppression of a meiotic division, thus maintaining a considerable degree of heterozygosity and accounting for the normal viability of the diploids.

Other physiological effects have been mentioned occasionally without the claim that they represent the ultimate cause of the low viability of haploids. Both O. Hertwig (1913) and Böök (1941) stress the slow and weak contractions of the heart, a condition which may well be a secondary consequence of the reduced vigor rather than its cause. On the other hand, Bataillon found that parthenogenetic frog embryos are more susceptible to heat than are diploid embryos (cf. Rostand, 1938).

From the foregoing it is obvious that little progress can be expected in the analysis of the effects of haploidy until both the structure and the function of haploid organs are investigated much more thoroughly.

Polyploidy. The viability of triploid salamander larvae is normal, on the whole. In *Triturus viridescens* and *Amblystoma mexicanum*, the two species in which the largest numbers of triploids have been obtained, the rate of mortality is not significantly higher than in the controls. Some triploid larvae of *Triturus viridescens*, *T. pyrrhogaster*, and *Eurycea bislineata* show a slightly higher growth rate when abundant food is offered, as was mentioned earlier. It would be interesting to find out whether this is connected with a greater food intake or with a better utilization of the food during digestion. In later stages of larval development triploids may show a greater tendency to develop ascites, a localized accumulation of fluid in the body cavity as contrasted with the generalized edema of haploids. However, ascites could by no means be regarded as a general symptom of triploidy.

The slight increase in growth rate shown by some triploid larvae that were fed "maximally" suggested special experiments to test the reaction of triploid and diploid larvae to pituitary stimulation (Fankhauser and Watson, 1945). Large larvae of *Triturus viridescens*, two to four weeks before the normal time of metamorphosis (first molt), were implanted with three or four adult pituitaries, at intervals of from eight to ten days. The rather paradoxical effect of this treatment was a great delay and partial inhibition of metamorphosis, as had been found by Herre (1935) and Herre and Rawiel (1939) in similar experiments with larvae of *Triton*. Resorption of the gills and tailfin was slow and incomplete. The animals never showed any tendency to leave the water permanently, although several reached an age of six to eight months, and two lived for two and nearly three years, respectively. The two latter had reached an apparently permanent, partially metamorphosed condition with rudimentary gills, fairly wide tailfin, and a pigment pattern quite distinct from that of normal animals. In the implanted animals the first molt took place six to eight weeks later than in the controls, but molting continued as long as the animals lived, in some cases at short and fairly regular intervals of from two to five days.

Growth continued during the first few months but ceased later, in the two animals which lived beyond the first year. Whether or not the growth was at first accelerated in comparison with unimplanted controls is difficult to determine, since the latter, in nature, remain on land after metamorphosis for one to two years as "red efts" and, when raised in the laboratory in terraria, do not take food for some time, and later show considerable individual variations in feeding response and growth rate.

As far as could be determined from the observation of the living animals, both the metamorphic and the growth reactions to pituitary stimulation were identical in triploid and diploid animals. Ten weeks after the first implant the average length of ten diploid animals was 43.6 mm., that of nine triploid animals was 42.7 mm. Under the conditions of these experiments the additional growth hormone thus failed to produce greater stimulation in the triploids.

With the addition of more sets of chromosomes the viability decreases. Tetraploid as well as pentaploid larvae are less vigorous than triploids and usually develop ascites (Fig. 6: 2), which may increase with age or disappear completely later on. In general, their reactions to mechanical stimulation are slower, and the food intake is more or less reduced. In one pentaploid larva, in which the progress of digestion of *Enchytraeus* worms was more closely watched, it was definitely slower than in the diploids, as measured by the rate of passage through the stomach and intestine.

A physiological effect which seems to be typical for young pentaploid larvae of *Triturus viridescens* is a greater susceptibility to a 1:5000 solution of chloretone, which is used as an anesthetic during photography. Prolonged exposure to this solution has no ill effects on diploid larvae, while two pentaploids showed the typical effects of an overdose of chloretone, characterized by a bending of the main stems of the gills and an almost complete reduction of the gill branches. In both cases no recovery took place, and the general condition of the animals made it necessary to preserve them.

The rate of heart beat was measured repeatedly in a tetraploid and several pentaploid larvae and was found to be approximately normal. The single pentaploid *Triturus pyrrhogaster* observed so far was definitely more vigorous than pentaploids of *T. viridescens*. It never developed ascites and reacted more promptly to various forms of stimulation. It is quite probable that in this species both a decrease and an increase in chromosome number have less effect than in others.

Detailed observations have been made on heteroploid parthenogenetic tadpoles of *Rana nigromaculata* by Kawamura (1939a). He gives his animals the following rating with regard to viability: (1) diploids, (2) triploids and tetraploids, (3) haploids and hexaploids. It must be mentioned, however, that the majority of all parthenogenetic tadpoles in his experiments were very abnormal, regardless of chromosome number.

There is practically no information available on the physiological effects of polyploidy in triploid and tetraploid races of arthropods. Their general viability may be assumed to be normal, since they compete successfully with the diploid races. Artom (1925) merely mentions that in *Artemia* tetraploidy has "important physiological manifestations." I have not been able so far to find an elaboration of this general statement. Vandel (1934) notes that in the isopod, *Trichoniscus elisabethae*, one triploid male lived for two and a half years while diploid males rarely reach their second year.

The rapidly growing literature on the physiological effects of polyploidy in plants will be reviewed briefly in the concluding section, since it suggests various lines of future investigations with animals. In connection with the observations on polyploid salamander larvae just mentioned, it is interesting to note here that haploid plants are also less viable as a rule, that tetraploid individuals may show greater vigor than the diploid (e. g., *Cuthbertia*, Giles, 1942; *Sedum*, H. E. Smith, 1943), while octoploid plants are generally weaker (e. g., *Nicotiana*, Greenleaf, 1938; H. H. Smith, 1943) or cannot be obtained at all (*Datura*, Blakeslee, 1941).

(d) "Qualitative" effects

The effects of heteroploidy on amphibian development discussed so far have been primarily quantitative, largely direct consequences of changes in cell size. Are there also modifications of a more qualitative character, striking abnormalities of development which might be considered as typical for the various changes in chromosome number? The distinction between quantitative and qualitative changes is, of course, often arbitrary. A modification of the proportions of the body or of certain organs, for instance, is based on

quantitative alterations that have been of different magnitude in different dimensions. The end result, however, as expressed in the appearance of the developing embryo or larva, is clearly qualitative. The same reasoning applies to changes in the size of single organs, changes which appear purely quantitative when considered alone, but qualitative when viewed from the standpoint of the final effect, which is a distinct pathological condition.

TABLE 9

Abnormalities found in haploid embryos and larvae of amphibians

	SPECIES	AUTHOR
Broader head and body	*Triton taeniatus*	P. Hertwig, 1916, Baltzer, 1922, Fankhauser, 1937a (Fig. 6)
	Triton palmatus	Fankhauser, 1937a (Fig. 7)
Dorsal flexure of body, widening of tail	*Rana pipiens*	Rugh, 1939
Shorter gills	*Bufo, Rana*	G. Hertwig, 1913
	Triton taeniatus	O. Hertwig, 1913, P. Hertwig, 1923
	Triturus viridescens	unpublished
Deformed lower jaw	*Triturus viridescens*	unpublished
	Triturus pyrrhogaster	Fankhauser, 1937a, Kaylor, 1940a
Circulation seldom functional	*Rana pipiens*	Porter, 1939
Neural plate one-third shorter	*Rana pipiens*	Porter, 1939
Microcephaly	*Rana fusca*	Dalcq, 1932
	Rana pipiens	Rugh, 1939
Abnormal development of brain	*Rana pipiens*	Porter, 1939
	Triton taeniatus	P. Hertwig, 1923
Small or abnormal eyes	*Rana pipiens*	Porter, 1939
	Rana fusca	Dalcq, 1932
	Triton taeniatus	P. Hertwig, 1923, Böök, 1941
	Triton palmatus	Fankhauser, 1937a

The main types of abnormalities that have been noted specifically in haploid amphibian embryos and larvae are summarized in Table 9. Most frequent are changes in body proportions, shortening of the gills, and deficiencies in the nervous system, particularly in the brain and the eyes. These last mentioned deficiencies are perhaps all connected with difficulties in gastrulation and consequent deficient induction in the head region. Two points must be emphasized: (1) all these abnormalities also appear in diploid embryos, although more rarely; and (2) among the haploids they appear more or less frequently and vary greatly in degree. They are not constant symptoms always associated with haploidy, except perhaps in certain species, e. g., the shortening of the neural plate and the abnormal development of the brain and eyes in *Rana pipiens* embryos, according to Porter (1939). As a whole, the abnormalities are less frequent and less severe in newt embryos than in those of frogs, as was emphasized by O. Hertwig (1913) and has been substantiated by more recent observations on species of *Triturus*. Some haploid newt larvae are completely normal in appearance as long as they live. Whether or not any particular abnormal condition occurs in anurans but not in urodeles, or vice versa, remains an open question.

Triploid salamander larvae show the same types of abnormalities as diploid larvae, and with about the same frequency. No typical morphological

peculiarities have been found. The number of tetraploid larvae observed so far is too small for any general conclusions. The two tetraploids of *Eurycea bislineata* were essentially normal, aside from their slower growth and greater tendency to develop ascites, mentioned earlier. The tetraploid larva of *Triturus viridescens* showed a temporary fusion of the first three digits of the forelimbs which disappeared during later stages. At this time the posterior portion of the tail began to curve to the left and, at metamorphosis, formed a tight coil (Fig. 5: 7).

A curvature of the body axis appears to be typical for older pentaploid larvae. The process usually begins in the tail region and may be caused in part by the excessive width of the tailfin, whose ventral edge bends over in contact with the bottom of the culture dish. Later on the trunk itself shows a more or less pronounced S-curve (Fig. 6: 3–5). Such axial curvatures occur but rarely in diploid larvae and may be typical for animals with four or more sets of chromosomes. This conclusion is supported by the fact that similar, though less extreme, curvatures were found in a pentaploid larva in each of two other species, *Triturus pyrrhogaster* (Fig. 6: 7–8) and *Amblystoma mexicanum*. The cause of this phenomenon may perhaps be found in unequal growth rates of different tissues of the axis, possibly a more rapid elongation of the notochord.

Temporary fusion of some of the digits was also observed in three of the four pentaploids that developed to metamorphosis. In older pentaploid larvae of *Triturus viridescens* the head is definitely more pointed than in the diploid. Altogether, these distinguishing characteristics of larvae with higher chromosome numbers seem to be primarily due to local disturbances of growth patterns.

Changes of a more qualitative nature have also been described in polyploid arthropods. In tetraploid embryos of *Artemia* the outer margin of the head is straight instead of rounded as in the diploid (Artom, 1927). Octoploid *Artemia* have a shorter caudal fork with fewer bristles; higher salt concentrations, which shorten the fork of diploid animals, cause it to be completely absent in the octoploid (Gross, 1932). Triploid *Drosophila* differ from the diploid in the proportions of their body rather than in size and are characterized by a stocky build (Dobzhansky, 1937). Vandel (1927) notes that triploid individuals of the isopod *Trichoniscus* have a purplish color, while the diploids are orange or light brown. Triploid females of the wasp *Habrobracon* are often abnormal in appearance (A. R. Whiting, 1928; Torvik, 1931) and may have irregular abdominal sclerites (Inaba, 1939).

Changes in the proportions of various organs are frequently noted in polyploid plants. In general, the organs of tetraploids are coarser (cf. Kostoff, 1938). The leaves, in particular, are broader and thicker (cf. Müntzing, 1936), as was already mentioned by Winkler (1916) for tetraploid tomato seedlings. This change in shape can be traced back to the leaf initials, which are broader and maintain this difference throughout ontogeny (maize, Randolph, Abbe, and Einset, 1944; *Vinca rosea*, Cross and Johnson, 1941). In *Datura* there is a progressive shortening and thickening of the capsules from the haploid to the octoploid condition (Blakeslee, 1941). The shape of the fruit is also modified in tetraploid cucurbits (Sinnott and Blakeslee, 1938; Shifriss, 1942). Shifriss also noted an accentuated serration of the leaf margin in *Cucumis*.

Octoploid plants are frequently abnormal. In *Nicotiana* they show general monstrosity; the dying leaf tips in particular demonstrate that octoploids are close to the upper end of the range of chromosome numbers compatible with development (Greenleaf, 1938). Microscopical study reveals a general disorganization of the cells and tissues in parts of the leaves (H. H. Smith, 1943).

6. *Effects on sex differentiation*

From the beginning of these studies on polyploidy in amphibians, it was hoped that they might throw some light also on the interesting and controversial subject of sex determination. In contrast to the great volume of work devoted to the embryology and physiology of sex differentiation in this class of vertebrates, the number of papers dealing with the genetics of sex is very limited. There are several good reasons for this: lack of knowledge of heritable variations which would offer an approach through studies on sex linkage, absence of clear-cut visible differentiation of the sex chromosomes, and considerable lability of the genetic sex, which is easily modified by non-genetic factors, at least in some species. Much of the work is still concerned with the primitive question whether the male or female is heterogametic.

The available evidence on the genetical basis of sex is derived mainly from the following sources:

(1) Breeding experiments with occasional her-

maphroditic frogs and with "differentiated" and "undifferentiated" local races, the results of which are most easily explained on the assumption that the male is heterogametic, XY, the female homogametic, XX (Crew, 1921; Witschi, 1923, 1929, 1934).

(2) Investigation of the gonads of diploid parthenogenetic tadpoles and frogs that lived beyond the stage of sex differentiation (Loeb, Parmenter, Kawamura; cf. review in Tyler, 1941). Since both males and females have been found, the facts derived from this source do not support the assumed female homogamety without some supplementary hypothesis involving the ontogenetic lability of the original sex.

(3) Experiments on sex reversal have furnished the most decisive information in two instances. Removal of the testes of male toads allows the normally present rudimentary ovaries or Bidder's organs to produce mature ova, which may be fertilized by spermatozoa from normal males. According to Ponse (1930, 1941) the offspring from such crosses are all males, a fact which strongly suggests male homogamety in toads. In the salamander *Amblystoma*, an ovary of a genetic female may be completely transformed into a testis under the influence of a grafted testis that was transplanted as a gonad rudiment in an early embryonic stage and is finally removed after transformation of the host gonad has taken place. If a sex-reversed female is mated with a normal one, females and males appear in the offspring in the ratio of three to one. This can be explained on two assumptions, (1) that the female is heterogametic, WZ (or XY), and (2) that WW (or YY) individuals are viable and normal females (WZ × WZ = 1 WW + 2 WZ + 1 ZZ). Actually, it could be shown that one-third of the female offspring are of WW constitution, since they produce female offspring exclusively when mated to normal males, while the remaining two thirds give a normal sex ratio (Humphrey, 1942a, b, 1945).

The value of polyploid individuals in the study of sex determination has been amply demonstrated by the work of Bridges on *Drosophila* intersexes and "supersexes," which are the product of abnormal combinations of sex chromosomes and sets of ordinary chromosomes, or autosomes. Triploid flies are either normal females or intersexes, but never normal males, since the normal ratio of one X-chromosome to two sets of autosomes that is present in diploid males cannot be obtained. Investigation of the gonads of the first four triploid individuals of *Triturus viridescens* that were raised to metamorphosis at once indicated that the sex chromosome mechanism of salamanders is different from that of the fruitfly, since one animal possessed normal appearing testes, while the other three contained under-developed ovaries that were much smaller and less advanced in differentiation than those of diploid controls. The total number of germ cells was reduced to about one-third of the normal (Fankhauser, 1940a). This situation is similar to that found in moths, where triploids are either normal males or females with rudimentary ovaries or with more or less intersexual gonads. For moths, the heterogamety of the females has been established beyond doubt previously through studies on sex-linkage (cf. the review by Cockayne, 1938). The conclusion was obvious, therefore, that in newts also the female possesses an unequal pair of sex chromosomes (WZ), while the male is homogametic (ZZ).

Since the time of publication of this first account many more triploid larvae of *Triturus viridescens* have been raised to metamorphosis for a detailed study of their gonads, a study now in progress. Some of these animals are spontaneous triploids that either have normal appearing testes, or, in the majority of cases, more or less rudimentary ovaries. The far greater number of triploids were experimentally induced by cold or heat treatment of eggs. These induced triploids are practially all females with rudimentary ovaries; only two males have been found so far in a total of over forty animals (Griffiths, 1941; and unpublished observations).

These facts can be explained most easily by the assumptions that the female sex is heterogametic, and that the first meiotic division is equational for the sex-differentiating segments of the W and Z (or X and Y) chromosomes in most of the eggs. The second maturation spindle would thus usually contain a W and a Z chromosome, and suppression of the second maturation division by cold or heat would produce almost exclusively eggs of the constitution WZ which, fertilized by normal Z-bearing sperms, would give rise to WZZ individuals (cf. Fankhauser, 1942).

For a complete analysis of the influence of triploidy on sex it would be essential to study the later development of the gonads. The initial difficulties encountered in the raising of metamorphosed newts into the red eft stage have largely

been overcome at present. Furthermore, older gonads are available in the pituitary-implanted, semi-permanent larvae mentioned earlier, where the reactions of the gonads to excessive pituitary stimulation may be studied. A preliminary survey of these slides has shown that the triploid ovaries reacted differently from the diploid as regards both size and structure.

Because of the probable existence of opposite sex determining mechanisms in different taxonomic groups of amphibians it was important to study the effects of triploidy in other species of salamanders. In *Triturus pyrrhogaster*, sex differentiation is not always clear-cut at the time of metamorphosis. Only two cold-induced triploids could be sexed so far. Both possessed ovaries of normal or approximately normal size and histological appearance (unpublished observations of Rita C. Watson). This is in good agreement with Kaylor's findings (1943) that a triploid animal of possibly androgenetic origin had larger ovaries than the controls. More observations are needed to demonstrate conclusively that the gonads of this species react to triploidy in a different way from those of the common eastern newt.

A number of spontaneous triploid larvae of the two-lined salamander, *Eurycea bislineata*, which in nature metamorphoses during the third year, were raised to ages ranging from five to nine months. Four possessed normal testes; five had underdeveloped ovaries or rudimentary gonads of questionable sex. A detailed study of these cases has not yet been made.

As soon as Humphrey announced the demonstration of female heterogamety in *Amblystoma* on the basis of abnormal sex ratios in the progeny of sex-reversed genetic females, it appeared highly desirable to test the effects of triploidy in the same species. The axolotl offers the added advantages of being easily raised to sexual maturity in the laboratory and of having been subjected to a far-going experimental analysis of the phenomena of sex differentiation by Humphrey and others. Refrigeration experiments with axolotl eggs proved at once successful in inducing triploidy (Fankhauser and Humphrey, 1942), and a considerable number of triploids have been obtained, some of which are being raised. A preliminary check of the gonads shows that females again predominate. However, males appear more frequently than in experimental triploids of *Triturus viridescens*, a fact which indicates that the first maturation division may be reductional for the differential segments of the sex chromosomes in a considerable percentage of the eggs. In older triploids the condition of the ovaries varies greatly between individuals and may approach the normal in size and differentiation. Whether or not the later development of triploid testes is normal has not been established as yet.

Theoretical considerations concerning the genetics of sex in salamanders in general would be premature before the available material, including the gonads of tetraploid and pentaploid individuals, has been analysed in detail and more cases have been added. Interesting information may be expected from triploid axolotls with different combinations of sex chromosomes, viz., WZZ, WWZ, and WWW, all of which should be obtainable by refrigerating eggs from the offspring of sex-reversed females.

The possibilities of this approach to the analysis of sex determination in amphibia will not be adequately utilized until it is applied to frogs and toads. The only information on triploid anurans available so far is that obtained by Kawamura (1939b, 1940) on five parthenogenetic individuals of *Rana nigromaculata* and *Rana japonica*, including four advanced tadpoles and one metamorphosed frog. Two of these contained rudimentary ovaries; three possessed more abnormal gonads with few or no germ cells. The interpretation of these observations is not clear, since three of the four diploid parthenogenetic frogs also had degenerated or under-developed ovaries and because, furthermore, most of the parthenogenetic individuals were abnormal in various other respects. Kawamura suggests that abnormal trophic conditions exist in all parthenogenetic animals, to which a triploid constitution of the tissues adds further disturbances of the physiological conditions that interfere with the normal growth of the ovaries.

This survey of the influence of changes of chromosome number on sex would not be complete without a mention of the conditions found in haploid or partially haploid animals. The haploid *Triton taeniatus* that developed from an egg fragment containing a sperm nucleus and was raised to metamorphosis (Baltzer, 1922) contained small but unmistakable ovaries (Fankhauser, 1938b). This fact agreed with the expectation based on the *Drosophila* type of sex determination with female homogamety. No other pure haploids have been raised sufficiently far since then; however, several

advanced haploid-diploid mosaic individuals have been examined. In one case (*Triturus pyrrhogaster*, Kaylor, 1943) in which haploid and diploid cells were mixed rather irregularly, the right gonad was a normal ovary, the left, possibly haploid, gonad a poorly developed ovary. In two bilateral haploid-diploid mosaic larvae of *Amblystoma* the gonad on the haploid side was a testis (Humphrey and Fankhauser, 1943). One of these was a gynandromorphic animal in which the diploid gonad on the right side, originally an ovary, had been transformed almost completely into a testis under the influence of the male gonad on the haploid side.

If we assume female heterogamety to be the rule among salamanders, androgenetic animals (with a paternal set of chromosomes) would all be expected to be males. The occurrence of ovaries in an androgenetic newt might be explained by some special supplementary hypothesis as well as by invoking the modifying action of some nongenetic factor. In any interpretation we have to keep in mind constantly the apparently narrow margin between the male and female sex balance in amphibians and the close homology between the W and Z chromosomes, demonstrated by the fact that, in *Amblystoma*, WW and ZZ individuals are fully viable and identical in all respects except sex.

C. CHANGES INVOLVING ONE OR MORE INDIVIDUAL CHROMOSOMES ("ANEUPLOIDY")

Individuals with one or more chromosomes added to the normal diploid complement, or with one or more chromosomes missing, are found rather frequently in plants. In the jimson weed, *Datura*, it was early shown that the addition of each individual chromosome of the haploid set of twelve has different characteristic effects on the appearance of the plant, so that twelve distinct types of "trisomic" plants occur (Blakeslee, Belling, and Farnham, 1920; Blakeslee and Belling, 1924). Similar observations were made later on trisomics of *Nicotiana sylvestris* (Goodspeed and Avery, 1939), in tomatoes (Lesley, 1928), and in maize. Aneuploids with two or more extra chromosomes are in general less viable or fail to appear altogether. As the number of additional chromosomes is increased to the point where they constitute an almost complete third set, the plants again become vigorous since, in such hypo-triploid plants, the total balance of genes approaches the normal sufficiently to be compatible with normal development. However, different species of plants vary greatly in their susceptibility to chromosome unbalance; in cultivated varieties of hyacinths, for instance, most aneuploid chromosome numbers between the diploid (sixteen) and the tetraploid are known (de Mol, 1921; Darlington and Mather, 1944).

Among animals, aneuploidy is a much rarer phenomenon. It has been studied most extensively in *Drosophila*, where the effects of changes involving single chromosomes again depend on the kind of chromosome involved and are closely related to its size. Addition of a small fourth chromosome produces slight changes in the external appearance of the flies, e. g., in the shape of the wings and bristles, while subtraction of the same chromosome causes changes in an opposite direction as well as a pronounced retardation of development and decrease in viability. A third X-chromosome greatly reduces the viability of the larvae and pupae and causes modification of various structures in the surviving adult flies. Flies with one of the large second or third chromosomes added or missing have not been found so far. Presumably they are not viable because of the serious disturbance of the normal balance of genes (cf. Li, 1927).

In species with higher haploid chromosome numbers than *Drosophila*, changes involving a single chromosome would be expected to have less serious consequences. A strain of the grasshopper, *Trimerotropis citrina* (N = 12), was found to carry an extra first chromosome, apparently without striking changes in viability or appearance (Carothers, 1941). In another species of grasshoppers, *Mecostethus grossus*, Callan (1941) found one male, externally normal, in which the third largest autosome was present three times in all mitoses examined. In several species of American land snails, with haploid chromosome numbers ranging from seventeen to thirty-one, individuals or races with 2N + 1, 2N − 1, or 2N − 2 chromosomes occur (Husted, 1943).

Among our salamander larvae six aneuploid individuals have been found so far. One larva of *Triturus viridescens*, developed from an untreated egg, possessed twenty-four chromosomes (2N + 2). It was delayed in development and characterized by a large flat head, small eyes, and poor circulation; it never fed. Both the pigment cells and the blood cells of the living larva were larger than normal. The tailtip regenerated very slowly and showed an irregular, ragged edge. In addition, heart and viscera showed complete situs inversus. Another aneuploid individual of the same species, a hypo-diploid (2N − 3), was much re-

tarded in development, very abnormal from the neurula stage on, and died early. There was pronounced microcephaly, grossly defective circulation, and general deformity of the trunk and tail.

A single hyper-diploid individual (2N + 3 or 4) appeared among larvae of *Triturus pyrrhogaster* that developed from refrigerated eggs (Fankhauser, Crotta and Perrot, 1942). It showed extreme microcephaly and edema along with other abnormal features (Fig. 7: 6). Three hypo-diploid larvae (2N − 3 or 4) were produced in refrigeration experiments with axolotl eggs. All three were abnormal and inviable.

Kawamura (1939a) found a single hyper-diploid individual (probably 2N + 4) among 413 parthenogenetic larvae of *Rana nigromaculata*. It too was clearly abnormal, with strongly curved body and deformed tail.

Although the number of aneuploid amphibian larvae observed so far is small, the fact that all have been abnormal and non-viable seems to indicate that either addition or subtraction of two or more chromosomes is incompatible with normal development. On the other hand, none of the various abnormalities shown by the aneuploids were distinctive, since they also occur among diploid larvae. It is possible, however, that the particular combination of symptoms shown by each larva was typical for its chromosome constitution, because they all differed from one another in their appearance.

Zygotes with unbalanced chromosome complements may be formed more often than is indicated by the small number of aneuploid larvae identified so far. On the one hand, trisomic individuals, with a single chromosome present in triplicate, might be perfectly normal in appearance and viability, as they seem to be among grasshoppers, and would thus readily escape discovery. On the other hand, more extreme unbalance may lead to death at an early embryonic stage and account for a part of the "normal" mortality among amphibian embryos.

Most of the aneuploid plants described have been found among the offspring of triploids, in which meiosis produces spores with various abnormal chromosome combinations. There is no indication so far that any of the aneuploid salamander larvae were derived from a triploid parent, since they occurred singly among normal, diploid larvae, while a mating of a triploid with a diploid should produce a majority of offspring with irregular chromosome numbers. To date, meiosis has been studied in a single triploid salamander, the adult male newt discovered by Bŏŏk (1940, 1944). It showed the irregularities typical for autotriploid plants, with formation of univalents and trivalents in addition to bivalents. At metaphase II anywhere from four to twenty-one chromosomes were counted. However, there seemed to be a definite tendency towards formation of spermatids with an approximately haploid chromosome number. Many spermatids underwent pycnosis or developed into abnormal spermatozoa.

D. PARTIAL OR MIXED HETEROPLOIDY: CHROMOSOME MOSAICS

In addition to completely heteroploid amphibian larvae, individuals occur with two or more different chromosome numbers in different parts of the body, or in different cells in a single organ. This situation is of interest because it allows the close comparison of tissues with different chromosome numbers in a single individual and, furthermore, makes it possible to study the question whether certain effects of abnormal chromosome complements may be modified by the presence of normal, diploid cells or organs. Usually a part of the body of such mosaics is diploid; in some cases, however, all chromosome numbers are abnormal. Only two different kinds of chromosome complexes may be present, usually differing from one another by one or more complete sets ("euploid" mosaics). Or the body may represent a complex mixture of various, mostly aneuploid, numbers, which as a rule are the consequences of multipolar mitoses in early cleavage.

On this basis the chromosome mosaics may be divided into three groups: (1) euploid mosaics, in which each of the two chromosome numbers present is found in large areas of the body, or in large numbers of cells; (2) predominantly diploid individuals with one or more small polyploid areas; and (3) complex mosaics with highly irregular chromosome complements. Transitional conditions between these three groups also occur, but most cases may be classified without difficulty.

1. Euploid mosaics with wide distribution of two chromosome complexes ("chimeras")

Table 10 shows that among amphibian larvae such mosaics occur spontaneously as well as in various types of experiments, particularly after treatment of eggs to induce haploidy. Consequently, the majority of mosaics are partly haploid,

partly diploid. Various other combinations have also been found, such as haploid/triploid, diploid/triploid, etc.

Among the haploid/diploid larvae that have been studied more closely, one may again distinguish various types depending on the relative proportions of haploid and diploid cells and on the topographical arrangement of these cells. Some are predominantly haploid; in others, haploid and diploid cells occur with about equal frequency. In the latter, the body may be haploid on one side and diploid on the other, as in tadpoles developing from dispermic eggs of the frog and in some spontaneous and cold-induced mosaic salamander larvae, or the two kinds of cells may be found mixed irregularly in different parts of the body, as described, for instance, in a mosaic larva of *Triturus pyrrhogaster* (Kaylor, 1943). Various intermediate conditions occur, adding to the complexity of the situation. With the exception of bilateral mosaics, it is very unlikely that the same pattern of chromosome numbers will be found in two different individuals.

The mechanism responsible for the mosaic con-

TABLE 10

Types of chromosome mosaics ("chimeras") found among amphibian larvae

SPECIES	ORIGIN	NUMBER AND TYPES OF MOSAIC LARVAE	AUTHOR
Rana fusca	parthenogenesis	7 haploid/diploid, 4 haploid/diploid, 3 diploid/triploid	Hovasse, 1922 Parmenter, 1940
	polyspermy	regularly haploid/diploid	Herlant, 1911
Rana pipiens	parthenogenesis	3 haploid/diploid 1 diploid/triploid	Parmenter, 1933
	androgenesis	1 haploid/diploid 1 haploid/tetraploid 1 diploid/triploid	Porter, 1939
Rana palustris	parthenogenesis	1 haploid/diploid 1 diploid/triploid/tetraploid	Parmenter, 1933
Rana nigromaculata	parthenogenesis	8 haploid/diploid 3 haploid/triploid 1 haploid/pentaploid 1 triploid/hexaploid	Kawamura, 1939a
Triturus viridescens	spontaneous	1 haploid/diploid 1 haploid/triploid 1 diploid/hypertriploid	Fankhauser, 1941b
	cold treatment	6 haploid/diploid 1 haploid/triploid	Griffiths, 1941
		1 hyper-diploid/triploid 1 haploid/diploid	Fankhauser, 1942
Triturus similans	cold treatment	2 haploid/diploid	Costello, 1942
Triturus pyrrhogaster	androgenesis	1 haploid/diploid	Kaylor, 1940a, 1943
Eurycea bislineata	spontaneous	3 haploid/diploid	Michalski, 1942
Axolotl	spontaneous cold treatment	2 haploid/diploid 2 haploid/diploid 1 triploid/pentaploid 1 diploid/pentaploid	Humphrey and Fankhauser, 1943, and current experiments

dition is definitely known in a few instances only. In dispermic frog's eggs, the chromosome pattern is determined by the simultaneous division of the diploid fusion nucleus and the accessory sperm nucleus which remains separated from the former. Haploid and diploid cells, as well as cells with both a haploid and a diploid nucleus are formed during early cleavage, which is more or less irregular. The presence of binucleate cells leads to various complications later on, including abnormal mitoses and failure of further cell divisions in that area.

As a whole, bilateral mosaic larvae may be recognized more easily than other types because of the asymmetrical development of the body, which is curved towards the haploid side or shows delayed differentiation of that side. In some cases the difference in the number and size of the melanophores in corresponding areas is also very striking. Differences in pigmentation are particularly obvious in mosaic axolotl larvae derived from matings between dominant black and recessive white individuals which differ in a single pair of genes, if the chromosome set on the haploid side is contributed by the white parent; under these circumstances it is also possible to determine within limits the mode of origin of the mosaic condition. In both cases studied so far the haploid set was paternal, either brought in by a second sperm nucleus which divided independently (dispermy), or derived from an early division of a single sperm nucleus into two haploid nuclei one of which fused with the egg nucleus to produce the diploid side ("partial fertilization").

The possible modes of origin of parthenogenetic mosaic larvae have been discussed by Parmenter (1933) and Kawamura (1939a, pp. 202, 206, 208), who consider various mechanisms: duplication of the haploid chromosome set in one or more blastomeres during early cleavage through a monocentric mitosis, retention of a second set of maternal chromosomes during maturation followed by a delayed fusion with one of the descendants of the haploid egg nucleus, etc.

The fate of mosaic larvae varies greatly and is probably determined in part by the proportion and distribution of the types of cells with different chromosome complexes. Both bilateral and more irregular mosaics may survive to metamorphosis. An example of the first type, described by Griffiths (1941), is given by the haploid/triploid *Triturus viridescens*, which was predominantly haploid on the left side. Kaylor's (1940, 1943) haploid/diploid mosaic of *Triturus pyrrhogaster* is a representative of the second type. The viability is thus much improved over that of haploids, a fact which offers possibilities for the future analysis of the causes of haploid nonviability. Careful study of a number of mosaics may show whether their viability is dependent on the diploid constitution of any particular organ or tissue (cf. King and Slifer, 1934, p. 609). Furthermore, mosaics may survive past the stage of sex differentiation to furnish more material for the investigation of the sex of haploid gonads (cf. p. 101).

In this connection it is of interest that haploid/diploid mosaics may also be produced artificially by uniting complementary parts of a haploid and a diploid gastrula (Hadorn, 1935, 1937). Some of the conditions obtaining in such "chimeras" can also be reproduced by connecting a haploid embryo with a diploid in parabiosis in early tailbud stages (Kaylor, 1940b).

The literature on chromosome "chimeras" and gynandromorphism in other animals will be discussed in another publication.

2. Diploid animals with small polyploid areas

Amphibian larvae of this type may easily escape detection unless the tailfin contains a polyploid sector. So far, only two diploid larvae have been found in which the fin included a small tetraploid area (*Triturus pyrrhogaster*, Fankhauser, Crotta, and Perrot, 1942). The study of complete serial sections through numerous larvae and animals in metamorphosis has not furnished any evidence for such limited, partial polyploidy. Various organs of adults should be investigated with regard to their chromosome complement; however, it does not seem likely that certain organs or tissues are regularly polyploid, or at least partly polyploid ("polysomaty"), a condition found in many plants and insects and also described for the liver of the rat (Beams and King, 1942; Sulkin, 1943; Biesele, 1944).

3. Complex mosaics with irregular chromosome numbers

("Poikiloploidy," Levy, 1920b; "multiform aneuploidy" Böök, 1944).

In contrast to larvae possessing cells of two different, usually euploid chromosome constitutions, mosaic animals of this category show a wide range of irregular chromosome numbers in their cells. In the tailfin of parthenogenetic frog tadpoles Levy (1920b) found mitoses with anywhere

from eight to twenty-four chromosomes, while haploid and diploid cells were very rare. This observation has not been duplicated in more recent work by various investigators; in any case there is no evidence for a general lability of the chromosome number in the tailfin.

There are obvious reasons why larvae with irregular chromosome numbers in a large proportion of their cells should be rare, although an irregular distribution of chromosomes may be expected whenever abnormal and particularly multipolar mitoses take place during cleavage or later stages of development. The fact is well established that the development of an egg does not proceed normally beyond the gastrula stage if multipolar mitosis occurred at the first or a later cleavage division. This was first demonstrated by Boveri's (1902, 1907) work on dispermic eggs of sea urchins, where the first cleavage mitosis usually has three or four poles between which the chromosomes are distributed at random.

Multipolar mitoses are frequently found in eggs or egg fragments of salamanders undergoing androgenetic development, i. e., from which the egg nucleus has been removed. Fertilization in urodeles is normally polyspermic, but the further development of the accessory sperm nuclei is arrested at the time of the first division of the diploid fusion nucleus through some inhibiting influence originating from the diploid mitotic system (Fankhauser, 1932a; Fankhauser and Moore, 1941a). When this inhibiting mechanism is removed, some of the accessory sperm nuclei divide independently. However, the nuclear and centrosomal components of the mitotic cycle are frequently out of gear, so that various types of abnormal mitosis are found. As a result, relatively few egg fragments or operated eggs develop into purely haploid embryos. The mortality is particularly high during cleavage and in the blastula and gastrula stages. When preserved at the critical stage, such eggs usually show a mosaic of irregular chromosome numbers in most or all of the dividing cells; frequently they also contain cells with asters but without chromosomes (egg fragments of *Triturus viridescens* and *Triton palmatus*, Fankhauser, 1932b, 1934b; whole eggs of *Triturus viridescens*, Fankhauser and Kaylor, 1935; Fankhauser and Moore, 1941b; Kaylor, 1941).

In egg fragments of *Triton palmatus* a more detailed analysis of the composition of the abnormal chromosome complexes was possible than in dispermic sea urchin eggs, because of the large size of the cells and chromosomes and the striking morphological individuality of the latter. In many abnormal sets, although they contain more than the haploid number of chromosomes, certain chromosomes are completely absent while others are represented two or three times, a situation creating an extreme disturbance of the normal balance of the genes. Some complements with the normal haploid chromosome number were also found to be very abnormal in composition. The make-up of such highly abnormal sets reveals a complex mitotic history that must have included a whole chain of abnormal mitoses of various types.

All observations on amphibian eggs are thus still in agreement with Boveri's conclusion that, from the gastrula stage on, a complete haploid set of chromosomes is required for normal development to take place. This is indicated also by the negative results of experiments to obtain sub-haploid frog embryos by fertilizing eggs with radiated or trypaflavinated sperm and attempting to eliminate some maternal chromosomes from the maturation spindle by mechanical means (Dalcq, 1932). In addition, the actual composition of the abnormal complexes with more than the haploid number of chromosomes provides evidence for Morgan's suggestion (1927, pp. 204, 656) that the presence of some chromosomes in duplicate or triplicate may be as disturbing in its effects on development as their complete absence.

E. GENERAL PROBLEMS

1. The relative unimportance of specific cell size in amphibian development

One of the main results of these studies on heteroploidy in amphibians is the demonstration that embryonic and larval development are relatively independent of cell size. Although the average cell size in a given tissue is typical for the species, the dimensions of the individual building blocks may be changed well beyond the limits of the normal range of variation found in diploid individuals without any serious interference with development. We may say, then, that the complex processes of early vertebrate development and organogenesis may proceed normally, on the whole, not only with cells of the normal size two, typical for the diploid condition, but also with units of the sizes one, three, four, or five.

This finding eliminates one of the hypotheses regarding the relative scarcity of polyploidy among animals repeatedly suggested, most recently by von Wettstein (1940, p. 386). He assumes that the complicated processes of the embryonic development of animals, like gastrulation, must be dependent on such a delicate balance between cell size, cell number, and rate of cell division that any marked change of these values would necessarily lead to disturbances that should be much more serious than in plants, with their simpler conditions of development.

It is quite possible that the detailed microscopical study of pentaploid larvae preserved in various stages of development will show some deviations from the normal path of development. However, there can be no doubt that a typical salamander larva, with all its complex and coordinated activities, can be built from cells that are two and one-half times larger than normal. Whether still larger cells are compatible with normal development is not known. Kawamura's (1939a) hexaploid frog tadpoles were very abnormal; but so were many of his triploid and diploid parthenogenetic larvae. The fact that octoploid races of the brine shrimp *Artemia* occur in nature cannot be taken as a sure indication that octoploid vertebrate embryos are viable, particularly in view of the fact that in plants the upper limit seems to be reached or passed in octoploid individuals.

2. The maintenance of normal body size in polyploid larvae through adjustment of cell number

A second striking phenomenon is the absence of gigantism among polyploid salamander larvae, a fact which shows that the typical body size is maintained as far as possible under a variety of disturbing conditions. At every level of polyploidy, from the triploid to the pentaploid, the increase in cell size is compensated by a corresponding decrease in cell number. Therefore, the body size that is typical for the species cannot be determined by a genetically fixed ceiling on cell number, or at least not by this factor alone. Cell number is controlled by other factors the nature of which is not known with certainty as yet, although several possibilities suggest themselves:

(1) Various investigators have proposed that a constant body size could be obtained automatically, irrespective of chromosome number, if the rate of cell division were to change in inverse proportion to cell size. Indirect evidence obtained from the study of the rate of regeneration in triploid larvae, which is normal, does not support this view, as far as triploidy is concerned. The lower growth rate and the slower progress of regeneration in pentaploid larvae demonstrate a lower rate of cell division but do not tell whether this is a primary attribute of the polyploid cells or a secondary consequence of a decreased physiological efficiency of the polyploid organism. It will be necessary to test the rate of mitosis of polyploid cells in tissue culture, where they are removed from any control of the body as a whole.

(2) A second factor is suggested by the important rôle in growth control played by the pituitary. If the production of growth hormone were to decrease more and more as the chromosome number increases, or if polyploid tissues were less reactive to the same concentration of the hormone than the diploid, the size of the body might be kept within normal limits. The preliminary experiments reported in this paper did not show any significant difference in the reactivity of diploid and triploid larvae to implants of adult pituitaries. It will be of great interest in the future to attempt an assay of the various pituitary hormones produced by polyploid animals, since a functional deficiency of the pituitary might also express itself in the development of the gonads.

(3) The maintenance of normal body size may also be an expression of the adaptive power of the amphibian embryo, which is well known for its ability to achieve a normal or nearly normal development in spite of the most drastic attempts of the experimenter to interfere with it. The mechanisms that underly this regulative ability are still unknown. That it also has a controlling influence on the size of the body is strongly suggested by the growth of diploid salamander larvae developed from half-eggs or from isolated blastomeres that, at the time of hatching, are approximately half the normal size but approach the typical size of the species as they reach metamorphosis.

The existence of some regulatory genetic mechanism governing total organ size rather than body size in certain plants has been suggested by Sinnott and Franklin (1943) to explain the normal size of the mature fruit in tetraploid cucurbits. However, the regulation in this case is secondary, since the tetraploid fruit primordium is about twice as large as the diploid, but loses this initial advantage

because of a reduced expansion of the cells during the later stages of growth.

3. *The maintenance of normal form of organs through changes in cell shape*

The subordination of individual cells to a more general controlling mechanism is demonstrated with particular clarity when a structure of a polyploid larva cannot reach normal configuration through an adjustment of cell number alone. Where cells are arranged in a single layer to form a small tube, as in pronephric tubules, the thickness of the wall cannot be kept constant, with larger cells, except by changes in their shape. Preliminary observations on pronephric tubules of young larvae have shown that both the size of the cross-section of the tubule and the diameter of its wall are approximately the same in haploid, diploid, and pentaploid individuals. This is accomplished by a progressive flattening of the individual cells with increasing chromosome number so that a cross section of a pentaploid tubule comprises two cells on the average, while in a diploid tubule one may find from three to six. Similar changes in cell shape are found in the epidermis and may be expected in other thin layers of cells. In this connection, mention should again be made of the changes that have been described recently in the shape of the cell of the apical meristem of tetraploid plants (*Vinca rosea*, Cross and Johnson, 1941), although in this case the wider cells of the tetraploid are responsible for the greater width of the stem and of the leaf primordia rather than for the preservation of normal form.

4. *Specific, qualitative effects of polyploidy and their theoretical interpretation*

The existence of qualitative differences between diploid and polyploid plants is beyond doubt, although their importance and frequency have received widely divergent estimates from different workers. According to Darlington (1937), the same chromosome complement always has a qualitative as well as a quantitative effect when represented different numbers of times. Müntzing (1936, p. 281), on the other hand, emphasizes that tetraploid plants are mainly magnified editions of the diploid, although certain differences may occur that are not strictly quantitative. Certain abnormalities that may be classified as qualitative changes have been noted in haploid and pentaploid amphibian larvae. They appear to be caused largely by local changes in growth patterns. However, it is likely that more detailed investigations will bring out more numerous and more varied deviations from the normal condition.

The existence of qualitative differences between polyploid and diploid individuals is of great theoretical interest since, at first sight, the multiplication of all the genes of the complement, maintaining a normal gene balance, would not be expected to change the final effect of the genotype. Various suggestions have been made to explain these qualitative effects. First of all, the possibility should be mentioned that, in polyploid organisms, one may have to differentiate between the action of the genes themselves and that of the total mass of "chromatin," which seems to be mainly responsible for the increase in nuclear and cell size and thus creates different spatial conditions for the activity of the former (cf. Lindstrom, 1936; Goldschmidt, 1937). Special studies of this dual effect of polyploidy are needed, although they may not be very profitable until the relations between genes and "chromatin" are better understood.

Several authors have stated in general terms that qualitative changes may be expected because an increase in chromosome number produces a new genetic system. More specifically, the expression of the genes may be different in a polyploid for any one of the following reasons or a combination of them:

(1) Some genes may produce their maximum effect in double dose, while others do not; in the polyploid, the action of the former would not be enhanced, while the latter would show a cumulative action (Randolph and Hand, 1938, 1940, p. 63; Goldschmidt, 1938, p. 152).

(2) Genes with cumulative action in turn may vary greatly in the extent to which additional alleles will enhance their expression. With some, the increase in total effect may be small; with others, doubling of the gene number may more than double the effect, as in the case of the gene for yellow endosperm color in corn, where the tetraploid shows a fivefold increase in the amount of carotenoid per cell (Randolph and Hand, 1940).

(3) The cytoplasmic substrate with which the gene products finally interact may be limited in amount for some genes, but present in excess for others, a condition which would again produce a differential effect on gene expression in the polyploid (cf. Goldschmidt, 1938, p. 152).

(4) If the diploid is heterozygous for any number

of factor pairs, addition of a third set of genes may change the dominance relations at different loci to different degrees. Some genes, in single dose, are completely dominant over two recessive alleles; others are not. In the tetraploid, on the other hand, if it is produced by chromosome doubling, the dominance relations should be similar to those in the diploid.

5. *Physiological effects of polyploidy*

Recent studies on polyploid plants emphasize more and more the importance of physiological changes produced by the increase in chromosome number. Many of these physiological effects are interrelated or connected with morphological modifications. Brief summaries may be found in Müntzing (1936), Cain (1944, chapters 27 and 28) and O'Mara (1942). Here it will suffice to list some of these observations to demonstrate the character and variety of physiological consequences of polyploidy:

(1) increase in concentration of various important substances, such as vitamin C in tetraploid tomatoes (Sansome and Zilva, 1933) and in triploid apples (Crane and Zilva, 1931; Müntzing, 1936, p. 367), nicotine in tetraploid tobacco (Naguti, Okuma, and Oka, 1939), carotenoid in the endosperm of tetraploid corn (Randolph and Hand, 1938, 1940), sugar, ascorbic acid and colloidal nitrogen in tetraploid cabbage (Barr and Newcomer, 1943), carotene and anthocyanin in flowers of tetraploid snapdragons and other species (Straub, 1940);

(2) decrease of ash in tetraploid tomatoes (Kostoff and Axamitnaja, 1935);

(3) decrease in osmotic pressure of cell sap in heteroploid mosses (Becker, 1931) and in *Vinca* (Taylor, 1942);

(4) changes in rate of water absorption and transpiration in tetraploid *Vinca* (Taylor, 1942);

(5) changes in the rate of photosynthesis and of carbon-dioxide production per unit of leaf surface (cf. Kostoff, 1938),

(6) changes in photoperiodism (female sterility of tetraploid rye under natural short days of January and February, O'Mara, 1942),

(7) increased resistance to attack by fungus in triploid aspen, *Populus tremula* (Nilsson-Ehle, 1936),

(8) greater adaptability to environmental conditions, particularly to different soils, and thus wider geographic range (cf. Cain, 1944, chapter 29),

(9) change from self-incompatibility to compatibility in fertilization in tetraploid Petunia (Stout and Chandler, 1941).

These observations suggest a multitude of studies on the physiology of polyploid amphibians or other vertebrates, studies which should also include typically animal functions, e. g., the biochemistry of the blood; digestion, excretion, and glandular activity with particular regard to the endocrines; the physiology of the nervous system in the presence of fewer but larger cells, with emphasis on the rate of transmission of impulses, the activity of sense organs, and learning ability. In short, any function in which cell size and cell number may play a rôle would be worth investigating in polyploid individuals. It is unfortunate that tetraploids occur rarely and cannot yet be produced experimentally, since they would constitute more favorable material than triploids because of the greater magnitude of the primary effects.

6. *Sex determination in vertebrates*

The fact seems well established at present that among amphibians both male heterogamety (XY/XX sex chromosomes of frogs) and female heterogamety (WZ/ZZ chromosomes of toads and salamanders) occur. Whether or not there are exceptions to this rule in either or both of the two groups remains an open question. It is not unlikely that opposite sex chromosome mechanisms may be found in related species, as is the case in cyprinodont fishes. Of great interest in this connection are Gordon's (1945) recent observations on *Platypoecilus maculatus*, in which XY chromosomes are present in wild populations and WZ chromosomes in domesticated breeds. These findings suggest the possible existence of geographical races with contrasting sex chromosome mechanisms in some species of amphibians, a condition which would offer an explanation of the observations on *Triton taeniatus* discussed earlier in this paper. The ovarian character of the gonads of the single androgenetic haploid raised to metamorphosis in Switzerland would be in agreement with the expectation based on female heterogamety as found in *Drosophila*. The normal maleness of the single adult triploid found in Sweden, on the other hand, can be accounted for easily on the basis of male homogamety and corroborates our observations on *Triturus viridescens* and other species. However, as long as the exceptional

situation of the haploid remains an isolated case it may well find an entirely different explanation.

In salamanders the differentiation of the W and Z chromosomes from the autosomes and from one another has not proceeded very far, as is shown by their morphological identity and Humphrey's discovery that an axolotl of the constitution WW is a viable, normal salamander, identical with a ZZ individual aside from the primary and secondary sex characteristics. The W and Z chromosomes may be largely homologous except for a short differential segment carrying the genes that trip the balance in a male or female direction. Moreover, the normal appearance and activity of the ovaries of a WW female also show that the Z chromosome cannot carry any important female determining factors in its differential segment.

Further work on the sex of polyploid amphibia should also yield information on the relative distribution of male- and female-determining genes in the sex chromosomes and autosomes, a situation which must remain unknown unless the two types of chromosomes can be matched in various polyploid combinations. Although observations on the single class of Amphibia could not provide a sound basis for general conclusions regarding the distribution of "sex genes" in the chromosome complement of vertebrates as a whole, they would in all probability present a closer approach to the situation in birds and mammals than the classical investigations on insects and dioecious plants.

7. Heteroploidy and cancer

Deviations from the normal chromosome number have often been described in tumor cells and have been suggested repeatedly as one of the factors responsible for the transformation from the normal to the malignant state. Following Boveri's lead (1914), the importance of multipolar and other abnormal forms of mitosis producing highly irregular chromosome complements was emphasized in earlier investigations. In recent years the occurrence of polyploidy in tumor cells has been given renewed attention and was supplemented by the discovery that endomitosis may produce polyvalent chromosomes that may or may not separate into their component units to increase the total number of chromosomes (cf. Biesele, Poyner, and Painter, 1942). The study of these nuclear phenomena is also particularly significant in the analysis of the early stages of experimental carcinogenesis that mark the transition from the normal to the precancerous condition (Biesele and Cowdry, 1944).

For investigations of this nature amphibians offer obvious advantages, first, because of the large size of their cells and chromosomes, and secondly, because of the knowledge that is already available regarding the effects of multipolar mitosis and polyploidy in normal tissues. Little is known at present concerning the reactions of amphibian tissues to carcinogens (cf. Needham, 1942, p. 239 ff.). Preliminary investigations of the effects of the subcutaneous application of methyl-cholanthrene on the skin of adult newts (*Triturus viridescens*) showed an early hyperplasia of the epidermis in the region of the implant, followed by the appearance of a large swelling that regressed later on, with extensive necrosis in the subcutaneous connective tissue (Hilton, 1942; Crecca and Warner, 1944). The prompt and pronounced reaction of the epidermis offers favorable material for chromosome studies. Whether the effects are temporary or may lead to malignant changes is unknown. In either case they are worth investigating, because of the possible connection between any peculiarities in the reaction to carcinogens on the one hand, and the extensive power of regeneration of adult salamanders and the general theory of organizers in amphibian development on the other, as has been pointed out by Waddington (1935) and Needham (1936, 1942).

Furthermore, whatever the nature of the effects of carcinogens in amphibians, once they are well analysed in diploid individuals it will be possible to apply the substances to polyploids and to compare their reactions with those of the former. This comparison would be of considerable interest from the standpoint of the mechanisms that underlie the early changes leading to tumor formation (cf. Cowdry, 1943), since it would reveal whether the size of the cells, or the quantity of chromosome material present, has any influence on these processes.

8. Allopolyploidy and "allo-haploidy" (hybrid androgenesis)

In plants, doubling of the chromosome number may be superimposed on cross-fertilization between different species to produce "allotetraploid" or "amphidiploid" plants which combine characteristics of the two parent species with general features of tetraploids and represent distinct, fertile, and true-breeding types. No allopolyploid

animals have been found in nature or produced by experimental means so far. Refrigeration of freshly cross-fertilized amphibian eggs would be expected to produce triploids with one paternal and two maternal sets of chromosomes. Preliminary experiments with two species of Californian *Triturus* have not yet yielded significant results (Costello, 1942). In this connection it should again be mentioned that, depending on the particular combination of species used, hybridization in amphibians produces diverse results, ranging all the way from viable hybrids to haploid "false hybrids" that develop by gynogenesis with the maternal chromosomes alone. In the latter case, refrigeration of eggs may double the chromosome number from haploid to diploid (cf. Rostand, 1938).

Important results have already been obtained from experiments that are in part the reverse of those producing allopolyploids, viz., cross-fertilization followed by removal of the maternal set of chromosomes producing an androgenetic hybrid or, to use a term corresponding to allopolyploidy, an "allohaploid." The combination of the egg cytoplasm of one species of newt (*Triton*) with a haploid chromosome set of another does not give rise to viable larvae. Development comes to an end at various early stages, depending on the taxonomic relation of the two species used (Baltzer, 1920; P. Hertwig, 1922, 1923). However, in one combination analysed very fully the disharmony expresses itself primarily in a localized area, namely, the head-mesoderm, the breakdown of which causes the death of the embryo (Baltzer, 1930). If other regions of the androgenetic embryo are isolated in the gastrula stage and transplanted to normal, diploid embryos (Hadorn, 1932), or raised in vitro in salt solution (Hadorn, 1934), they may undergo complete histological differentiation. Transplants of epidermis may remain alive for months and, following metamorphosis, develop characteristics that are typical for the maternal species that contributed the cytoplasm (Hadorn, 1936). The conditions of such experiments would be somewhat simplified if a method were available for the induction of chromosome doubling in the "allo-haploid" egg in order to eliminate all disturbances that may arise from the haploid condition as such, rather than from the specific differences between cytoplasm and chromosomes.

SUMMARY

Amphibians are the only vertebrates in which the effects of changes in chromosome number have been studied so far. The results of these investigations are presented in this paper, with particular emphasis on the effects of heteroploidy on embryonic and larval development, and compared with observations on polyploid invertebrates and plants; these comparisons are not included in the summary.

A. Methods of identification of living heteroploid individuals

The chromosome number of young larvae may be determined directly by counts in dividing epidermis cells of the fin in a whole mount of the amputated tailtip. Secondary criteria of changes in chromosome number are: (1) the size of interphase nuclei in epidermis cells and other tissues, (2) the size of erythrocytes and of unicellular glands, (3) the spacing of epidermis and connective tissue nuclei, (4) changes in cell number in lateral line sense organs, (5) the number of nucleoli in interphase nuclei of epidermis cells, corresponding to the number of haploid chromosome sets present (clearly visible in axolotl tailtips only).

Before tailclipping, heteroploid larvae are often recognized by their distinctive pigment pattern, with larger but fewer melanophores as the chromosome number increases.

B. Addition and subtraction of whole chromosome sets (polyploidy and haploidy)

1. Frequency of spontaneous aberrations (Table 3)

Among larvae of the newt, *Triturus viridescens*, triploid individuals appear with a frequency of about 1.8 per cent, pentaploids occupy second place (ca. 0.28 per cent), haploids third (ca. 0.16 per cent). Tetraploid and aneuploid larvae, as well as chromosomal mosaics, occur more rarely. Similar deviations from the diploid chromosome number occur spontaneously in *Triturus pyrrhogaster*, *Eurycea bislineata*, and the axolotl.

2. The origin of spontaneous aberrations

Triploid individuals originate from the fusion of an unreduced, diploid gamete with a haploid one. It is probable that the egg contributes the extra set of chromosomes more frequently than the sperm. Whether tetraploid embryos are produced by the rare union of two diploid gametes, or by somatic doubling in the zygote, is unknown. Pentaploid

embryos are most likely produced by the fusion of a tetraploid egg, resulting from complete suppression of both maturation divisions, with a haploid sperm. Paternal inheritance of pigment pattern in one case shows that haploid axolotl larvae may develop by androgenesis. Less conclusive evidence indicates that other haploids develop with the maternal set of chromosomes, by gynogenesis or, possibly, parthenogenesis.

3. Experimental induction of changes in chromosome number

Haploid development of amphibian eggs may be induced by any one of the following methods: (a) parthenogenesis, (b) radiation or chemical treatment of spermatozoa before fertilization, (c) radiation of eggs before fertilization, (d) mechanical removal of egg chromosomes from fertilized eggs, (e) division of fertilized eggs into fragments, (f) application of cold or heat shortly after fertilization, (g) exposure of eggs to hydrostatic pressure.

Triploid embryos have been obtained in several species of salamanders by subjecting eggs immediately after fertilization to cold or heat to suppress the second maturation division, which is in metaphase at this time. Of all the larvae obtained so far from refrigerated eggs of *Triturus viridescens*, 78 per cent were triploid; among the larvae from heat-treated eggs, 71 per cent were triploid (Tables 5 to 8). Tetraploidy has not been induced experimentally so far.

Heteroploid embryos, including hexaploids, have also been obtained as by-products of unknown origin in experiments on parthenogenesis and androgenesis.

4. Primary effects of changes in number of chromosome sets

The size of the nuclei and cells increases approximately in proportion to the chromosome number (Table 2 and Fig. 1). Sufficiently accurate measurements of both nuclear and cell volume have not been made to determine whether the nucleoplasmic ratio remains constant at all levels of polyploidy. In some tissues heteroploid cells also show changes in shape.

5. Secondary effects

(a) *Body size.* The body size of polyploid amphibian larvae at comparable stages of development is always approximately the same, irrespective of chromosome number and cell size, since the latter is compensated by a corresponding reduction in cell number. Haploid larvae as a rule are smaller but show at least partial compensation in cell number.

(b) *Rate of development.* Haploid embryos develop more slowly than diploid. Whether the rates of growth and differentiation are affected to different degrees is not yet known. The growth rate of triploid salamander larvae is normal at first; in later stages of development it may or may not become slightly higher than in the diploid. In triploid *Triturus viridescens* the onset of metamorphosis is often delayed; the mean age at the first molt of 69 diploid animals was 89.4 days, that of 32 triploids was 102 days.

In tetraploid and, particularly, in pentaploid larvae of the same species differentiation, as judged by external features, is only slightly slower than in controls, while the growth rate is greatly reduced. Metamorphosis is delayed as a rule until the larvae have reached approximately the size typical for diploids at this stage.

(c) *Physiological effects.* The viability of haploid amphibian larvae is greatly reduced. Of thousands of haploids, only a few developed beyond the stage when feeding normally begins, and only a single one was raised to metamorphosis. The great majority of haploid larvae develop a more or less severe edema that is held by some to be the main cause of the lowered viability.

The viability of triploid salamander larvae appears to be normal. The few triploid newts that have been raised beyond metamorphosis seem to be as vigorous as the controls, as are some triploid axolotls which have been kept for over two years. Tests of the reactions of older diploid and triploid larvae of *Triturus viridescens* to implantation of adult pituitaries revealed no significant differences in growth rate or in other responses, with the exception of the gonads.

Tetraploid and pentaploid larvae are less vigorous and usually develop temporary ascites. As a whole their reactions are slower. Young pentaploid larvae seem to be more susceptible to the toxic effects of dilute chloretone solutions.

(d) *Qualitative effects.* Haploid embryos and larvae are usually characterized by changes in body proportions, shortening of the gills, and deficiencies in the nervous system, particularly in the brain and eyes. As a rule, these abnormalities are less severe in embryos of newts than in those of frogs.

Triploid salamander larvae do not show any morphological peculiarities. Older pentaploid lar-

vae develop a curvature of the body axis, beginning in the tail and sometimes leading to a tight coiling of the tail and pronounced S-curve of the whole body axis. In older pentaploid larvae of *Triturus viridescens* the head is more pointed than in the diploid. These abnormalities may be caused largely by local changes in growth patterns.

6. Effects on sex differentiation

At metamorphosis spontaneous triploids of *Triturus viridescens* possess either normal-appearing testes or more or less rudimentary ovaries with greatly reduced numbers of germ cells. The gonads of cold-induced triploids almost always are of the last mentioned type. These facts can be explained most easily by assuming that the female sex is heterogametic, and that the first maturation division is equational for the differential segments of the W and Z chromosomes in the great majority of eggs.

Spontaneous triploid larvae of *Eurycea bislineata* also are either normal males or females with rudimentary ovaries. In *Triturus pyrrhogaster*, on the other hand, triploid individuals at metamorphosis may have ovaries of normal size. The later development of triploid gonads has not been studied as yet, except in preliminary observations on axolotls which show that the condition of the ovaries varies greatly between individuals and may approach the normal.

Observations on haploid gonads are limited to four cases: a completely haploid, androgenetic *Triton taeniatus* which had small ovaries; a haploid/diploid mosaic larva of *Triturus pyrrhogaster* obtained in experiments on androgenesis, with a poorly developed, possibly haploid ovary on the left side; and two lateral haploid/diploid mosaic larvae of *Amblystoma*, in both of which the gonad on the haploid side was a testis.

C. Changes involving one or more individual chromosomes ("aneuploidy")

Seven hyper-diploid or hypo-diploid amphibian larvae have been found so far. All were abnormal and non-viable. Apparently, both addition and subtraction of two or more chromosomes are incompatible with normal development.

D. Partial or mixed heteroploidy: chromosome mosaics

1. Chromosomal mosaics or "chimeras" with two different, usually euploid, chromosome complexes in different regions of the body (haploid/diploid, haploid/triploid, diploid/triploid, etc.) occur spontaneously and in various experiments (Table 10). The proportion and the arrangement of the two types of cells vary greatly. Bilateral haploid/diploid mosaics are easily recognized among offspring from matings between dark and white axolotls if the haploid complement is derived from the white parent. As a rule, the viability of haploid/diploid mosaics is much better than that of pure haploids.

2. In two cases only, a small tetraploid area was found in the tailfin of an otherwise diploid larva. Such a condition might actually be more frequent but easily overlooked if the polyploid area were located in another part of the body.

3. Complex mosaics with irregular chromosome numbers result from the abnormal distribution of chromosomes in multipolar mitoses during early cleavage. Such eggs do not develop beyond the gastrula stage. Analysis of the composition of the abnormal chromosome complements shows that the majority are extremely unbalanced, with some chromosomes missing while others are represented two or three times. The presence of a complete, balanced set of chromosomes appears to be indispensable for amphibian development from the gastrula stage on.

E. General problems

1. Embryonic and larval development are relatively independent of cell size and may proceed normally, on the whole, not only with cells of the usual "size 2," typical for the diploid condition, but also with cells of sizes 1, 3, 4, or 5.

2. The adjustment of cell number that maintains an approximately normal body size in polyploid larvae in spite of the increase in cell size shows that the total cell number cannot be irrevocably fixed for the species, even within wide limits. The factors which may control cell number, and thus body size, are discussed briefly.

3. In organs with cells arranged in single layers, as in the tubules of the pronephros, the normal form may be maintained in polyploid larvae by changes in cell shape, viz., a progressive flattening of the individual cells with increasing chromosome number.

4. The theoretical importance of the occurrence of qualitative changes in polyploid organisms is discussed, particularly the question why multiplication of all the genes may produce changes in the expression of some genes and not of others.

5. Some physiological effects of polyploidy in plants are described briefly, since they suggest future physiological studies on polyploid animals.

6. The relations of polyploidy to sex in amphibians are discussed with regard to the problem of sex determination in vertebrates in general.

7. The occurrence and theoretical significance of heteroploidy in tumor cells indicate that diploid and polyploid amphibians may be favorable material for cytological studies of the early reactions of cells to carcinogens.

8. While polyploid species hybrids (allopolyploids) have not been studied in amphibians so far, interesting results have been obtained in experiments in which hybridization is followed by removal of the maternal chromosome set producing an androgenetic hybrid (or "allo-haploid"), with cytoplasm of one species and a haploid chromosome set of another in all its cells.

LIST OF LITERATURE

A. General articles on polyploidy

ARTOM, C. 1928. La polyploidie dans ses corrélations morphologiques et biologiques. *C. R. Soc. Biol. Paris*, 99, réunion plénière: 29–49.

BEAL, J. M. 1942. Induced chromosomal changes and their significance in growth and development. *Amer. Nat.*, 76: 239–252.

BLAKESLEE, A. F. 1941. Effect of induced polyploidy in plants. *Amer. Nat.*, 75: 117–135.

CAIN, S. A. 1944. *Foundations of Plant Geography*, Chapters 26–30. New York: Harper.

DARLINGTON, C. D. 1937. *Recent Advances in Cytology*. 2nd ed. Chapter 6. Philadelphia: Blakiston.

DOBZHANSKY, TH. 1941. *Genetics and the Origin of Species*. 2nd ed. Chapter VII. New York: Columbia Univ. Press.

GOODSPEED, T. H., and M. V. BRADLEY. 1942. Amphidiploidy. *Bot. Rev.*, 8: 271–316.

HEILBORN, O. 1934. On the origin and preservation of polyploidy. *Hereditas*, 19: 233–242.

HUSKINS, C. L. 1941. Polyploidy and mutations. *Amer. Nat.*, 75: 329–346.

LINDSTROM, E. W. 1936. Genetics of polyploidy. *Bot. Rev.*, 2: 197–220.

MÜNTZING, A. 1936. The evolutionary significance of autopolyploidy. *Hereditas*, 21: 263–378.

MULLER, H. J. 1925. Why polyploidy is rarer in animals than in plants. *Amer. Nat.*, 59: 346–353.

SANSOME, F. W., and J. PHILP. 1939. *Recent Advances in Plant Genetics*. 2nd ed. Chapters 5 to 8. Philadelphia: Blakiston.

SHARP, L. W. 1943. *Fundamentals of Cytology*. Chapter 14. New York: McGraw-Hill.

STEBBINS, G. L. 1940. The significance of polyploidy in plant evolution. *Amer. Nat.*, 74, 54–66.

——. 1942. Polyploid complexes in relation to ecology and the history of floras. *Amer. Nat.*, 76: 36–45.

VANDEL, A. 1937. Chromosome number, polyploidy, and sex in the animal kingdom. *Proc. Zool. Soc. Lond.*, 107A: 519–542.

VON WETTSTEIN, F. 1927. Die Erscheinung der Heteroploidie, besonders im Pflanzenreich. *Ergebn. Biol.*, 2: 311–356.

B. Special articles

ARTOM, C. 1923. Il tetraploidismo dei maschi dell' *Artemia salina* di Odessa in relazione con alcuni problemi generali di genetica. *Rend. Roy. Acad. Naz. dei Lincei*, 32: 505–507.

——. 1925. Gigantismo e costituzioni genetiche nell razze e nelle specie tetraploidi. *Riv. Biol.*, 7: 533–555.

——. 1927. Il diploidismo e il tetraploidismo dell' *Artemia salina*. *Verh. 5th Intern. Kongr. Vererb. Berlin*, 384–386.

——. 1929. Il differenziamento e l'accrescimento degli elementi nervosi dell'*Artemia salina* diploide e tetraploide durante lo sviluppo. *Bull. Ass. Anat.*, 24me réunion: 35–40.

ASTAUROV, B. L. 1940. *Artificial Parthenogenesis in the Silkworm (Bombyx mori L.)*. Moscow.

BALTZER, F. 1920. Ueber die experimentelle Erzeugung und die Entwicklung von *Triton*-Bastarden ohne mütterliches Kernmaterial. *Verh. Schweiz. Naturf. Ges., Neuenburg*.

——. 1922. Ueber die Herstellung und Aufzucht eines haploiden *Triton taeniatus*. *Verh. Schweiz. Naturf. Ges., Bern:* 248–249.

——. 1930. Ueber die Entwicklung des Tritonmerogons *Triton taeniatus* x *cristatus*. *Rev. Suisse Zool.*, 37: 325–332.

BARBER, H. N., and H. G. CALLAN. 1943. The effects of cold and colchicine on mitosis in the newt. *Proc. Roy. Soc. London, B*, 131: 258–271.

BARIGOZZI, C. 1941. Cytogenetical analysis of two wild populations of *Artemia salina* in connexion with polyploidism. *Proc. 7th Intern. Genet. Congr. Edinb.*: 57–58.

BARR, C. G., and E. H. NEWCOMER. 1943. Physiological aspects of tetraploidy in cabbage. *J. Agric. Res.*, 67: 329–336.

BARTHELMES, A. 1941. Mutationsversuche mit einem Laubmoos, *Physcomitrium piriforme*. I. Morphologische und physiologische Analyse der univalenten und bivalenten Protonemen einiger Mutanten. *Z. ind. Abst. Vererb.*, 79: 153–170.

BATAILLON, E. 1904. Nouveaux essays de parthénogénèse expérimentale chez les vertébrés inférieurs

(*Rana fusca* et *Petromyzon planeri*). *Arch. Entwmech. Org.*, 18: 1–56.

——— and TCHOU-SU. 1929. Analyse de la fécondation par l'hybridation et la polyspermie physiologique. *Arch. EntwMech. Org.*, 115: 779–824.

BEAMS, H. W., and R. L. KING. 1942. The origin of binucleate and large mononucleate cells in the liver of the rat. *Anat. Rec.*, 83: 281–298.

BECKER, G. 1931. Experimentelle Analyse der Genom- und Plasmon-wirkung bei Moosen. III. Osmotischer Wert heteroploider Pflanzen. *Z. ind. Abst. Vererb.*, 60: 17–38.

BIESELE, J. J. 1944. Chromosome complexity in regenerating rat liver. *Cancer Res.*, 4: 232–235.

——, and E. V. COWDRY. 1944. Chromosomal changes in epidermal carcinogenesis. *J. Nat. Cancer Inst.*, 4: 373–385.

——, H. POYNER, and T. S. PAINTER. 1942. Nuclear phenomena in mouse cancers. *Univ. Texas Publ.* 4243.

BLAKESLEE, A. F., and J. BELLING. 1924. Chromosomal mutations in the jimson weed, *Datura stramonium*. *J. Hered.*, 15: 194–206.

——, J. BELLING, and M. E. FARNHAM. 1920. Chromosome duplication and mendelian phenomena in *Datura* mutants. *Science*, 52: 388–390.

BÖÖK, J. A. 1940. Triploidy in *Triton taeniatus* Laur. *Hereditas*, 26: 107–114.

——. 1941. Induction of haploidy in a cold treatment experiment with egg cells of the salamander *Triton taeniatus*. *Kungl. Fysiogr. Sällsk. Lund. Förh.*, 11, no. 12: 1–16.

——. 1944. Personal communication.

BOVERI, TH. 1902. Ueber mehrpolige Mitosen als Mittel zur Analyse des Zellkernes. *Verh. phys. med. Ges. Würzburg, n. F.*, 35: 67–90.

——. 1905. Zellenstudien. V. Ueber die Abhängigkeit der Kerngrösse und Zellenzahl der Seeigel-Larven von der Chromosomenzahl der Ausgangszellen. *Jen. Z. Naturw.* 39 (n. F. 32): 445–524.

——. 1907. Zellenstudien. VI. Die Entwicklung dispermer Seeigeleier. Ein Beitrag zur Befruchtungslehre und zur Theorie des Kernes. *Jen. Z. Naturwiss.*, 43: 1–292.

——. 1914. *Zur Frage der Entstehung maligner Tumoren*. Jena.

BRAUNGART, D. C., and G. E. OTT. 1942. A cytological study of the effect of colchicine on *Drosophila melanogaster*. *J. Hered.*, 33: 163–165.

CALLAN, H. G. 1941. A trisomic grasshopper. *J. Hered.*, 32: 296–298.

CAROTHERS, E. E. 1941. Interspecific hybridization in the Acrididae (*Trimerotropis citrina* x *T. maritima*). *Genetics*, 26: 144.

COCKAYNE, E. A. 1938. The genetics of sex in Lepidoptera. *Biol. Rev.*, 13: 107–132.

COSTELLO, D. P. 1942. Induced haploidy and triploidy in Californian *Triturus*. *Anat. Rec.*, 84, no. 4: 60.

COWDRY, E. V. 1943. Experimental epidermal methylcholanthrene carcinogenesis in mice. *Biol. Symposia*, 10: 131–162.

CRANE, M. B., and S. S. ZILVA. 1931. The anti-scorbutic vitamin of apples. *J. Pomol. Hort. Sci.*, 9: 228–231.

CRECCA, R. W., and S. L. WARNER. 1944. The effects of methylcholanthrene on the integument of *Triturus viridescens*. Part II. Senior Thesis, Princeton University.

CREW, F. A. E. 1921. Sex-reversal in frogs and toads. A review of the recorded cases of abnormality of the reproductive system and an account of a breeding experiment. *J. Genet.*, 11: 141–181.

CROSS, G. L., and T. J. JOHNSON. 1941. Structural features of the shoot apices of diploid and colchicine induced tetraploid strains of Vinca rosea. *Bull. Torrey Bot. Club*, 68: 618–635.

DALCQ, A. 1930. La formule chromosomiale chez la grenouille. *Ann. Bull. Soc. Roy. Sci. Méd. nat. Bruxelles*, 1930: 15–21.

——. 1932. Contribution à l'analyse des fonctions nucléaires dans l'ontogénèse de la grenouille. IV. Modifications de la formule chromosomiale. *Arch. Biol. Paris*, 43: 343–366.

——, and S. SIMON. 1931. Contribution à l'analyse des fonctions nucléaires dans l'ontogénèse de la grenouille. III. Etude statistique et cytologique des effets de l'irradiation d'un des gamètes sur la gastrulation chez *Rana fusca*. *Arch. Biol. Paris*, 42: 107–165.

DARLINGTON, C. D., and K. MATHER. 1944. Chromosome balance and interaction in *Hyacinthus*. *J. Genet.*, 46: 52–61.

DOBZHANSKY, TH. 1929. The influence of the quantity and quality of chromosomal material on the size of the cells in *Drosophila melanogaster*. *Arch. EntwMech. Org.*, 115: 363–379.

DODDS, K. S. 1938. Chromosome numbers and spermatogenesis in some species of the hymenopterous family Cynipidae. *Genetica*, 20: 67–84.

DOOLEY, T. P. 1941. The influence of colchicine upon the germ cells of insects (Orthoptera) with special reference to the mitochondria and dictyosomes. *Trans. Amer. Micr. Soc.*, 60: 105–119.

EIGSTI, O. J. 1942. A comparative study of mitosis in diploid and tetraploid species. *Amer. J. Bot.*, 29: suppl., 7.

EINSET, J. 1942. Chromosome length in relation to transmission frequency of maize trisomics. *Genetics*, 28: 349–364.

——. 1944a. The occurrence of a tetraploid and two triploid apple seedlings in progenies of diploid parents. *Science*, 99: 345.

——. 1944b. Personal communication.

ERDMAN, L. H., and J. S. THOMPSON. 1943. Induction of triploidy in *Triturus viridescens* by heat-treatments. Senior Thesis, Princeton University.

FABERGÉ, A. C. 1936. The physiological consequences of polyploidy. I. Growth and size in the tomato. *J. Genet.*, 33: 365–382.

FANKHAUSER, G. 1925. Analyse der physiologischen Polyspermie des *Triton*-Eies auf Grund von Schnürungsexperimenten. *Arch. EntwMech. Org.*, 105: 501–580.

——. 1932a. Cytological studies on egg fragments of the salamander *Triton*. II. The history of the supernumerary sperm nuclei in normal fertilization and cleavage of fragments containing the egg nucleus. *J. Exp. Zool.*, 62: 185–235.

——. 1932b. The rôle of the chromosomes in the early development of merogonic embryos in *Triturus viridescens*. *Anat. Rec.*, 54, no. 3, suppl: 73.

——. 1934a. Cytological studies on egg fragments of the salamander *Triton*. III. The early development of the sperm-nuclei in egg fragments without the egg nucleus. *J. Exp. Zool.*, 67: 159–215.

—. 1934b. Idem. IV. The cleavage of egg fragments without the egg nucleus. *J. Exp. Zool.*, 67: 349–393.

——. 1934c. Idem. V. Chromosome number and chromosome individuality in the cleavage mitoses of merogonic fragments. *J. Exp. Zool.*, 68: 1–57.

——. 1937a. The production and development of haploid salamander larvae. *J. Hered.*, 28: 1–15.

——. 1937b. The development of fragments of the fertilized *Triton* egg with the egg nucleus alone ("gyno-merogony"). *J. Exp. Zool.*, 75: 413–469.

——. 1938a. The microscopical anatomy of metamorphosis in a haploid salamander, *Triton taeniatus* Laur. *J. Morph.*, 62: 393–413.

——. 1938b. Sex differentiation in a haploid salamander, *Triton taeniatus* Laur. *J. Exp. Zool.*, 79: 35–49.

——. 1938c. Triploidy in the newt, *Triturus viridescens*. *Proc. Amer. Philos. Soc.*, 79: 715–739.

——. 1939. Polyploidy in the salamander, *Eurycea bislineata*. *J. Hered.*, 30: 379–388.

——. 1940a. Sex differentiation in triploid newts (*Triturus viridescens*). *Anat. Rec.*, 77: 227–245.

——. 1940b. A pentaploid larva of the newt, *Triturus viridescens*. *Proc. Nat. Acad. Sci., Wash.* 26: 526–532.

——. 1941a. Cell size, organ and body size in triploid newts (*Triturus viridescens*). *J. Morph.*, 68: 161–177.

——. 1941b. The frequency of polyploidy and other spontaneous aberrations of chromosome number among larvae of the newt, *Triturus viridescens*. *Proc. Nat. Acad. Sci. Wash.*, 27: 507–512.

——. 1942. Induction of polyploidy in animals by extremes of temperature. *Biol. Symposia*, 6: 21–35.

——, R. CROTTA, and M. PERROT. 1942. Spontaneous and cold-induced triploidy in the Japanese newt, *Triturus pyrrhogaster*. *J. Exp. Zool.*, 89: 167–181.

——, and R. B. GRIFFITHS. 1939. Induction of triploidy and haploidy in the newt, *Triturus viridescens*, by cold-treatment of unsegmented eggs. *Proc. Nat. Acad. Sci. Wash.*, 25: 233–238.

——, and R. R. HUMPHREY. 1942. Induction of triploidy and haploidy in axolotl eggs by cold treatment. *Biol. Bull.*, 83: 367–374.

——, and ——. 1943. The relation between number of nucleoli and number of chromosome sets in animal cells. *Proc. Nat. Acad. Sci. Wash.*, 29: 344–350.

——, and C. T. KAYLOR. 1935. Chromosome numbers in androgenetic embryos of *Triturus viridescens*. *Anat. Rec.*, 64, no. 1, suppl. no. 1: 41–42.

——, and C. MOORE. 1941a. Cytological and experimental studies of polyspermy in the newt *Triturus viridescens*. I. Normal fertilization. *J. Morph.*, 68: 347–385.

——, and ——. 1941b. Idem. II. The behavior of the sperm nuclei in androgenetic eggs (in the absence of the egg nucleus). *J. Morph.*, 68: 387–423.

——, and R. C. WATSON. 1942. Heat-induced triploidy in the newt, *Triturus viridescens*. *Proc. Nat. Acad. Sci. Wash.*, 28: 436–440.

——, and ——. 1945. The effects of pituitary implants on diploid and triploid larvae of *Triturus viridescens* in premetamorphic stages. In press.

FLEMMING, W. 1879, 1880, 1882a. Beiträge zur Kenntnis der Zelle und ihrer Lebenserscheinungen. I, II, III. *Arch. mikr. Anat.*, 16: 302–436; 18: 151–259; 20: 1–86.

——. 1882b. *Zellsubstanz, Kern und Zelltheilung*. Leipzig.

FROLOVA, S. L. 1940. Cytology of development of parthenogenetic eggs of *Bombyx mori* L. activated by high temperature. *C. R. Acad. Sci. URSS*, 27: 604–606.

GILES, N. H. 1942. Autopolyploidy and geographical distribution in *Cuthbertia graminea* Small. *Amer. J. Bot.*, 29: 637–645.

GOLDSCHMIDT, R. 1931. Die sexuellen Zwischenstufen. *Berlin*.

——. 1937. Does the quantity of chromatin produce a genetic effect? *Amer. Nat.*, 71: 83–86.

——. 1938. *Physiological Genetics*. New York: McGraw-Hill.

GOODSPEED, T. H., and P. AVERY. 1939. Trisomic and other types in *Nicotiana sylvestris*. *J. Genet.*, 38: 381–458.

GORDON, M. 1945. The XY sex-chromosomes determine maleness in wild populations of *Platypoecilus maculatus* while the WZ determine femaleness in domesticated breeds of the same species. *Genetics*, 30: 6.

GREENLEAF, W. H. 1938. Induction of polyploidy in *Nicotiana* by hetero-auxin treatment. *J. Hered.*, 29: 451–464.

GREMILLION, D. F. 1942. Polyploidy in the germinal tissue of *Melanoplus femur-rubrum* (De G.). *Proc. Louisiana Acad. Sci.*, 7: 80–81.

GRIFFITHS, R. B. 1941. Triploidy (and haploidy) in the newt, *Triturus viridescens*, induced by refrigeration of fertilized eggs. *Genetics*, 26: 69–88.

GROSS, F. 1932. Untersuchungen über die Polyploidie und die Variabilität bei *Artemia salina*. *Naturwiss.*, 20: 962–967.

——. 1935. Die Reifungs- und Furchungsteilungen von *Artemia salina* im Zusammenhang mit dem Problem des Kernteilungsmechanismus. *Z. Zellforsch.*, 23: 522–565.

GUSTAFSON, F. G. 1944. Growth hormone studies of some diploid and autotetraploid plants. *J. Hered.*, 35: 269–272.

HADORN, E. 1932. Ueber Organentwicklung und histologische Differenzierung in transplantierten merogonischen Bastardgeweben. *Arch. EntwMech. Org.*, 125: 495–565.

——. 1934. Ueber die Entwicklungsleistungen bastard-merogonischer Gewebe von *Triton palmatus* (♀) x *Triton cristatus* ♂ im Ganzkeim und als Explantat in vitro. *Arch. EntwMech. Org.*, 131: 238–284.

——. 1935. Chimärische *Triton*larven mit bastard-merogonischen und normalkernigen Teilstücken. *Rev. Suisse Zool.*, 42: 417–426.

——. 1936. Uebertragung von Artmerkmalen durch das entkernte Eiplasma beim merogonischen *Triton*bastard, *palmatus* Plasma x *cristatus* Kern. *Verh. dtsch. zool. Ges., Freiburg*, 97–104.

——. 1937. Die entwicklungsphysiologische Auswirkung der disharmonischen Kern-Plasmakombination beim Bastard-merogon *Triton palmatus* (♀) x *Triton cristatus* ♂. *Arch. EntwMech. Org.*, 136: 400–489.

HASIMOTO, H. 1933. Genetical studies on the tetraploid female in the silkworm. *Bull. Imp. Sericult. Exp. Sta.*, 8: 359–381.

——. 1934. Id. II. Occurrence of tetraploid female in a gynandromorphous strain. *Bull. Imp. Sericult. Exp. Sta.*, 8: 505–514.

HERLANT, M. 1911. Recherches sur les oeufs di- et trispermiques de grenouille. *Arch. Biol. Paris*, 26: 103–335.

HERRE, W. 1935. Hypophysenimplantationen bei Marmormolchlarven. *Verh. dtsch. zool. Ges.*, 37: 65–75.

——, and F. RAWIEL. 1939. Implantation zusätzlicher Hypophysen in Larven verschiedener Molcharten. I. Die Wirkung auf die Geschlechtsorgane. *Arch. EntwMech. Org.*, 139: 86–109.

HERTWIG, G. 1913. Parthenogenesis bei Wirbeltieren, hervorgerufen durch artfremden, radiumbestrahlten Samen. *Arch. mikr. Anat.*, 81, II: 87–127.

——. 1918. Kreuzungsversuche an Amphibien. I. Wahre und falsche Bastarde. *Arch. mikr. Anat.*, 91: 203–271.

——. 1927. Beiträge zum Determinations- und Regenerationsproblem mittels der Transplantation haploidkerniger Zellen. *Arch. EntwMech. Org.*, 111: 292–316.

——, and P. HERTWIG. 1920. Triploide Froschlarven. *Arch. mikr. Anat.*, 94: 34–54.

HERTWIG, O. 1913. Versuche an *Triton*eiern über die Einwirkung bestrahlter Samenfäden auf die tierische Entwicklung. *Arch. mikr. Anat.*, 82, II: 1–63.

HERTWIG, P. 1916. Durch Radiumbestrahlung verursachte Entwicklung von halbkernigen *Triton*- und Fischembryonen. *Arch. mikr. Anat.*, 87, II: 63–122.

——. 1922. Bastardierung und Entwicklung von Amphibieneiern ohne mütterliches Kernmaterial. *Z. ind. Abst. Vererb.*, 27: 255–257.

——. 1923. Bastardierungsversuche mit entkernten Amphibieneiern. *Arch. EntwMech. Org.*, 100: 41–60.

HILTON, J. G. 1942. The effects of methylcholanthrene on the integument of Triturus viridescens. Senior Thesis, Princeton University.

HIRAIWA, Y. K., and T. KAWAMURA. 1936. Relation between maturation division and cleavage in artificially activated eggs of *Urechis unicinctus* (von Drasche). *Biol. Bull.*, 70: 344–351.

HIROBE, T. 1939. Polyploid silkworm induced by colchicine treatment upon eggs. *Jap. J. Genet.*, 15: 69–74.

HOERSTADIUS, S., and A. WOLSKY. 1936. Studien über die Determination der Bilateralsymmetrie des jungen Seeigelkeimes. *Arch. EntwMech. Org.*, 135: 69–113.

HOLTFRETER, J. 1943. Properties and functions of the surface coat in amphibian embryos. *J. Exp. Zool.*, 93: 251–323.

HOVASSE, R. 1922. Contribution à l'étude des chromosomes. Variations du nombre et régulation en parthénogénèse. *Bull. biol. France et Belg.*, 56: 141–229.

HUMPHREY, R. R. 1942a. Sex of the offspring fathered by two *Amblystoma* females experimentally converted into males. *Anat. Rec.*, 82, no. 3: 77.

HUMPHREY, R. R. 1942b. Sex reversal and the genetics of sex determination in the axolotl (*Amblystoma mexicanum*). *Anat. Rec.*, 84, no. 4: 15.

——. 1945. Sex determination in ambystomid salamanders: a study of the progeny of females experimentally converted into males. *Amer. J. Anat.*, 76: 33–66.

——, and G. FANKHAUSER. 1943. Two unusual haploid-diploid mosaics of mixed *Amblystoma*

mexicanum and *Amblystoma tigrinum* ancestry. *Anat. Rec.*, 87, no. 4: 23.

HUSTED, L. 1943. Personal communcation.

INABA, F. 1939. Polyploidy in *Habrobracon* induced by colchicine treatment. (A preliminary note). *Jap. J. Genet.*, 15: 344–347.

——. 1940. Polyploidy in *Habrobracon* induced by colchicine treatment. II. Production of impaternate females. *Jap. J. Genet.*, 16: 270–272.

KAWAGUCHI, E. 1936. Der Einfluss der Eierbehandlung mit Zentrifugierung auf die Vererbung bei dem Seidenspinner. I. Ueber experimentelle Auslösung der polyploiden Mutation. *J. Fac. Agric. (Sapporo)*, 38: 111–133.

KAWAMURA, T. 1939a. Artificial parthenogenesis in the frog. I. Chromosome numbers and their relation to cleavage histories. *J. Sci. Hirosima Univ., Ser. B, Div.* 1, 6: 115–218.

——. 1939b. Id. II. The sex of parthenogenetic frogs. *J. Sci. Hirosima Univ., Ser. B, Div. 1*, 7: 39–86.

——. 1940. Id. III. The development of the gonads in triploid frogs and tadpoles. *J. Sci. Hirosima Univ., Ser. B, Div. 1*, 8: 117–164.

KAYLOR, C. T. 1937. Experiments on androgenesis in the newt, *Triturus viridescens*. *J. Exp. Zool.*, 76: 375–394.

——. 1940a. Studies on experimental haploidy in salamander larvae. I. Experiments with eggs of the newt, *Triturus pyrrhogaster*. *Biol. Bull.*, 79: 397–408.

——. 1940b. Experiments on the parabiotic union of haploid and diploid larvae of *Triturus pyrrhogaster*. *Anat. Rec.*, 78, no. 4, suppl.: 52–53.

——. 1941. Studies on experimental haploidy in salamander larvae. II. Cytological studies on androgenetic eggs of *Triturus viridescens*. *Biol. Bull.*, 81: 402–419.

——. 1943. Sex differentiation in two androgenetic salamander larvae, *Triturus pyrrhogaster*. *Anat. Rec.*, 87: 127–139.

KEPPEL, D. M., and A. B. DAWSON. 1939. Effects of colchicine on the cleavage of the frog's egg (*Rana pipiens*). *Biol. Bull.*, 76: 153–161.

KING, R. L., and E. H. SLIFER. 1934. Insect development. VIII. Maturation and early development of unfertilized grasshopper eggs. *J. Morph.*, 56: 603–619.

KNAPP, E. 1939. Haploide Pflanzen von *Antirrhinum majus*. *Ber. dtsch. bot. Ges.*, 57: 371–379.

KOSTOFF, D. 1938. Directed hereditable variations conditioned by euploid chromosome alterations in higher plants. *Nature Lond.*, 142: 1117.

——, and I. A. AXAMITNAJA. 1935. Studies on polyploid plants. IX. Chemical analysis of diploid and their autotetraploid plants. *C. R. Acad. Sci. URSS*, 2, no. 34: 293–297.

LEHMANN, F. E., and H. WOKER. 1940. Verschwinden embryonaler Zellkerne von *Tubifex* nach Colchicinbehandlung. *Verh. Schweiz. Naturf. Ges., Locarno:* 181–182.

LESLEY, J. W. 1928. A cytological and genetical study of progenies of triploid tomatoes. *Genetics*, 13: 1–43.

LESLEY, M. M., and J. W. LESLEY. 1930. The mode of origin and chromosome behaviour in pollen mother cells of a tetraploid seedling tomato. *J. Genet.*, 22: 419–425.

LEVY, F. 1920a. Ueber die sogenannten Ureier im Froschhoden. *Biol. Zbl.*, 40: 29–37.

——. 1920b. Die Kernverhältnisse bei parthenogenetischen Fröschen. *Sitzber. Preuss. Akad. Wiss.*, 24: 417–425.

LI, JU-CHI. 1927. The effect of chromosomal aberrations on development in *Drosophila melanogaster*. *Genetics*, 12: 1–58.

MICHALSKI, J. V. 1942. Spontaneous aberrations in chromosome number (triploidy and haploidy) among larvae of the two-lined salamander, *Eurycea bislineata*. Ph.D. Thesis, Princeton University.

MICKEY, G. H. 1942a. Polysomaty and polyploid gametes in *Romalea microptera*. *Genetics*, 27: 156.

——. 1942b. Polyploid gametes in the Louisiana lubber grasshopper. *Proc. Louisiana Acad. Sci.*, 6: 82.

DE MOL, W. E. 1921. De l'existence de variétés hétéroploides de l'*Hyacinthus orientalis* L. dans les cultures hollandaises. *Arch. néerl. Sci. III B*, 4: 18–117.

MORGAN, T. H. 1927. *Experimental Embryology*. New York: Columbia Univ. Press.

——, C. B. BRIDGES, and A. H. STURTEVANT. 1925. The genetics of *Drosophila*. *Bibl. Genet.*, 2: 1–262

MÜNTZING, A. 1941. New material and cross combinations in *Galeopsis* after colchicine-induced chromosome doubling. *Hereditas*, 27: 193–201.

NAGUTI, Y., K. OKUMA, and H. OKA. 1939. Studies on the polyploidy in *Nicotiana* induced by the treatment with colchicine. I. General observations on the autotetraploid of *N. rustica* and *N. tabacum*. *Jap. J. Bot.*, 10: 309–319.

NAVASHIN, M. 1925. Polyploid mutations in *Crepis*. Triploid and pentaploid mutants of *Crepis capillaris*. *Genetics*, 10: 583–592.

NEEDHAM, J. 1936. New advances in the chemistry and biology of organized growth. *Proc. Roy. Soc Med.*, 29: 1577–1626.

——. 1942. *Biochemistry and Morphogenesis*. Cambridge: Cambridge Univ. Press.

NILSSON-EHLE, H. 1936. Ueber eine in der Natur gefundene Gigasform von Populus tremula. *Hereditas*, 21: 379–382.

OEHNINGER, M. 1913. Ueber Kerngrössen bei Bienen. *Verh. phys.-med. Ges. Würzburg*, 42: 135–140.

O'MARA, J. G. 1942. A photoperiodism accompanying autotetraploidy. *Amer. Nat.*, 76: 386–393.

PAINTER, T. S. 1923. Studies in mammalian spermatogenesis. II. The spermatogenesis of man. *J. Exp. Zool.*, 37: 291–336.

PARMENTER, C. L. 1933. Haploid, diploid, triploid, and tetraploid chromosome numbers and their origin in parthenogenetically developed larvae and frogs of *Rana pipiens* and *Rana palustris*. *J. Exp. Zool.*, 66: 409–453.

—. 1940. Chromosome numbers in *Rana fusca* parthenogenetically developed from eggs with known polar body and cleavage history. *J. Morph.*, 66: 241–260.

PINCUS, G., and H. SHAPIRO. 1940. Further studies on the parthenogenetic activation of rabbit eggs. *Proc. Nat. Acad. Sci. Wash.*, 26: 163–165.

—, and C. H. WADDINGTON. 1939. The effect of mitosis-inhibiting treatments on normally fertilized pre-cleavage rabbit eggs. *J. Hered.*, 30: 515–518.

PONSE, K. 1930. Le problème du sexe et l'évolution de l'organe de Bidder du crapaud. *Proc. 2nd Intern. Congr. Sex Res. Edinb.*: 202–210.

—. 1941. La proportion sexuelle dans la descendance issue des oeufs produits par l'organe de Bidder de crapauds femelles. (Note préliminaire). *Rev. Suisse Zool.*, 48: 541–544.

PORTER, K. R. 1939. Androgenetic development of the egg of *Rana pipiens*. *Biol. Bull.*, 77: 233–257.

RANDOLPH, L. F. 1941. Personal communication.

—. 1942. The influence of heterozygosis on fertility and vigor in autotetraploid maize. *Genetics* 27: 163.

—, E. C. ABBE, and J. EINSET. 1944. Comparison of shoot apex and leaf development in diploid and tetraploid maize. *J. Agric. Res.*, 69: 47–76.

—, and H. E. FISCHER. 1939. The occurrence of parthenogenetic diploids in tetraploid maize. *Proc. Nat. Acad. Sci. Wash.*, 25: 161–164.

—, and D. B. HAND. 1938. Increase in vitamin A activity of corn caused by doubling the number of chromosomes. *Science*, 87: 442–443.

—. 1940. Relation between carotenoid content and number of genes per cell in diploid and tetraploid corn. *J. Agric. Res.*, 60: 51–64.

RETZIUS, G. 1881. Studien über die Zellentheilung. *Biol. Untersuch.*, 1881: 109–134.

RHOADES, M. M. 1936. Note on the origin of triploidy in maize. *J. Genet.*, 33: 355–357.

RISMAN, G. C. 1942. Cell size in Habrobracon. *Genetics*, 27: 166.

ROBBINS, W. J., and V. KAVANACH. 1943. Growth of excised roots of polyploid tomatoes. *Amer. J. Bot.*, 30: 602–605.

ROSTAND, J. 1933. Influence du refroidissement sur le développement des oeufs hybrides *Bufo* ♀ x *Rana* ♂. *C. R. Soc. Biol. Paris*, 113: 346–347.

—. 1934. Gynogenèse du crapaud par refroidissement de l'oeuf. *C. R. Soc. Biol. Paris*, 115: 1680–1681.

—. 1936. Gynogenèse par refroidissement des oeufs chez Hyla arborea. *C. R. Soc. Biol. Paris*, 122: 1012–1013.

—. 1938. La parthénogenèse des vertébrés. *Act. Sci. Industr.*, no. 651. *Paris.*

ROTMANN, E. 1940. Die Bedeutung der Zellgrösse für die Entwicklung der Amphibienlinse. *Arch. EntwMech. Org.*, 140: 124–156.

RUGH, R. 1939. Developmental effects resulting from exposure to X-rays. *Proc. Amer. Philos. Soc.*, 81: 447–471.

—, and D. A. MARSLAND. 1943. The effect of hydrostatic pressure upon early development of the frog's egg (*Rana pipiens*). I. Macroscopic observations. *Proc. Amer. Philos. Soc.*, 86: 459–466.

SANSOME, F. W., and S. S. ZILVA. 1933. Polyploidy and vitamin C. *Biochem. J.*, 27: 1935–1941.

SATINA, S., A. F. BLAKESLEE, and A. G. AVERY. 1937. Balanced and unbalanced haploids in *Datura*. *J. Hered.*, 28: 192–202.

SEILER, J. 1927. Ergebnisse aus der Kreuzung parthenogenetischer und zweigeschlechtlicher Schmetterlinge. *Biol. Zbl.*, 47: 426–446.

—. 1936. Neue Ergebnisse aus der Kreuzung parthenogenetischer Schmetterlinge mit Männchen zweigeschlechtlicher Rassen. *Verh. disch. zool. Ges.*, 147–150.

—. 1937. Ergebnisse aus der Kreuzung parthenogenetischer und zweigeschlechtlicher Schmetterlinge. V. Die *Solenobia*-Intersexe und die Deutungen des Phänomens der Intersexualität. *Rev. Suisse Zool.*, 44: 283–307.

SHIFRISS, O. 1942. Polyploids in the genus *Cucumis*. *J. Hered.*, 33: 144–152.

SHKVARNIKOV, P. K. 1934. Ueber den Einfluss einzelner Chromosomen auf die Grösse der Zellen. *Biol. Zh.*, 3: 533–545.

SHULL, G. H. 1929. An unexpected association of factors belonging to three linkage groups of *Oenothera* and its explanation. *Proc. Nat. Acad. Sci. Wash.*, 15: 268–274.

SINNOTT, E. W., and A. F. BLAKESLEE. 1938. Changes in shape accompanying tetraploidy in cucurbit fruits. *Science*, 88: 476.

—, and A. H. FRANKLIN. 1943. A developmental analysis of the fruit in tetraploid as compared with diploid races of cucurbits. *Amer. J. Bot.*, 30: 87–94.

—, and V. V. TROMBETTA. 1936. The cytonuclear ratio in plant cells. *Amer. J. Bot.*, 23: 602–606.

SMITH, H. E. 1943. Polyploidy in *Sedum pulchellum*. II. Stomatal size and frequency. *Bull. Torrey Bot. Club*, 70: 261–264.

SMITH, H. H. 1943. Studies on induced heteroploids of *Nicotiana*. *Amer. J. Bot*, 30: 121–130.

SMITH, L. 1942. Cytogenetics of a factor for multiploid sporocytes in barley. *Amer. J. Bot.*, 29: 451–455.

SPEICHER, B. R. 1935. Cell size and chromosomal types in *Habrobracon*. *Amer. Nat.*, 69: 79–80.

——, and L. G. SPEICHER. 1940. The occurrence of diploid males in *Habrobracon brevicornis*. *Amer. Nat.*, 74: 379–382.

SPEMANN, H. 1914. Ueber verzögerte Kernversorgung von Keimteilen. *Verh. dtsch. zool. Ges., 24. Jahresvers., Freiburg i. Br.* 216–221.

——, and H. FALKENBERG. 1919. Ueber asymmetrische Entwicklung und Situs inversus viscerum bei Zwillingen und Doppelbildungen. *Arch. Entw-Mech. Org.*, 45: 371–422.

STALKER, H. D. 1942. Triploid intersexuality in *Drosophila americana* Spencer. *Genetics*, 27: 504–518.

STOUT, A. B., and C. CHANDLER. 1941. Change from self-incompatibility to self-compatibility accompanying change from diploidy to tetraploidy. *Science*, 94: 118.

STRAUB, J. 1940. Quantitative and qualitative Verschiedenheiten innerhalb von polyploiden Pflanzenreihen. *Biol. Zbl.*, 60: 659–669.

SULKIN, N. M. 1943. A study of the nucleus in the normal and hyperplastic liver of the rat. *Amer. J. Anat.*, 73: 107–125.

TÄCKHOLM, G. 1922. Zytologische Studien über die Gattung *Rosa*. *Acta Hort. Berg.*, 7: 97–381.

TAYLOR, J. H. 1942. A physiological study of diploid and related tetraploid plants. *Proc. Okla. Acad. Sci.*, 22: 137–138.

TCHOU-SU. 1931. Etude cytologique sur l'hybridation chez les anoures. *Arch. Anat. micr.*, 27: 1–105.

——. 1936. L'hybridation chez les anoures de Canton (Chine). *C. R. Acad. Sci. Paris*, 202: 242–244.

TORVIK, M. M. 1931. Genetic evidence for diploidism of biparental males in *Habrobracon*. *Biol. Bull.*, 61: 139–156.

TROMBETTA, V. V. 1942. The cytonuclear ratio. *Bot. Rev.*, 8: 317–336.

TYLER, A. 1941. Artificial parthenogenesis. *Biol. Rev.*, 16: 291–336.

VANDEL, A. 1927. Gigantisme et triploidie chez l'isopode *Trichoniscus* (*Spiloniscus*) *provisorius* Racovitza. *C. R. Soc. Biol. Paris*, 97: 106–108.

——. 1928. La parthénogenèse géographique. *Bull. Biol. France Belg.*, 62: 164–281.

——. 1934. Id. II. Les mâles triploides d'origine parthénogénétique de *Trichoniscus* (*Spiloniscus*) *elisabethae* Herold. *Bull. Biol. France Belg.*, 68: 419–463.

WADDINGTON, C. H. 1935. Cancer and the theory of organizers. *Nature*, 135: 606–608.

WAGNER, C. E. 1944. Experiments on artificial parthenogenesis of eggs of the newt *Triturus viridescens*. Senior Thesis, Princeton University.

WARMKE, H. E., and A. F. BLAKESLEE. 1939. Induction of simple and multiple polyploidy in *Nicotiana* by colchicine treatment. *J. Hered.*, 30: 419–432.

VON WETTSTEIN, F. 1937. Experimentelle Untersuchungen zum Artbildungsproblem. I. Zellgrössenregulation und Fertilwerden einer polyploiden *Bryum*-Sippe. *Z. ind. Abst. Vererb.*, 74: 34–53.

——. 1940. Idem. II. Zur Frage der Polyploidie als Artbildungsfaktor. *Ber. dtsch. bot. Ges.*, 58: 374–388.

WHITING, A. R. 1928. Genetic evidence for diploid males in *Habrobracon*. *Biol. Bull.*, 53: 438–449.

WINKLER, H. 1916. Ueber die experimentelle Erzeugung von Pflanzen mit abweichenden Chromosomenzahlen. *Z. Bot.*, 8: 417–531.

WITSCHI, E. 1923. Ueber die genetische Konstitution der Froschzwitter. *Biol. Zbl.*, 43: 83–96.

——. 1929. Studies on sex differentiation and sex determination in amphibians. III. Rudimentary hermaphroditism and Y chromosome in *Rana temporaria*. *J. Exp. Zool.*, 54: 157–223.

——. 1934. Genes and inductors of sex differentiation in amphibians. *Biol. Rev.*, 9: 460–488.

WOKER, H. 1943. Phasenspezifische Wirkung des Colchicins auf die ersten Furchungsteilungen von *Tubifex*. *Rev. Suisse Zool.*, 50: 237–243.

——. 1944. Die Wirkung des Colchicins auf Furchungsmitosen und Entwicklungsleistungen des *Tubifex-Eies*. *Rev. Suisse Zool.*, 51: 109–171.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will frequently appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to B. H. Willier, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, Homewood Campus, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

GENERAL BIOLOGY

GENERATION OF ANIMALS. *Loeb Classical Library.* *By Aristotle. Translated by A. L. Peck. Harvard University Press, Cambridge, Mass.; Wm. Heinemann, London.* $2.50 (cloth); $3.50 (leather). lxxviii + 608 pp. 1943.

This is indeed a welcome addition to the Loeb Classical Library, for the *De Generatione Animalium* has been strangely neglected by translators in comparison with the *Historia Animalium*. The only recent translation into English of the former treatise, that made by Arthur Platt in 1910, can hardly bear contrast with D'Arcy Thompson's masterly translation of the *Historia*. It is rare indeed that so happy a combination of classical scholarship and biological knowledge as Thompson's can be found to undertake the translation of the great biological works of antiquity. Dr. Peck, of Christ's College, Cambridge, makes no claim to a professional knowledge of biology, but it is evident, from his preface and footnotes, that he has profited much by discussion with Joseph Needham and other biologists of his university. That he is himself a classical scholar of discernment is equally apparent in the excellent introduction, in which Aristotle's natural philosophy of causes is discussed, along with the varied meanings to be given to such key words as *Logos, Arche, Physis, Dynamis, Pneuma*, and *Psyche*; in the description and evaluation of the MS sources and emendations; in the footnotes and appendices, which serve admirably to clarify Aristotle's views; and, most important of all, in the translation itself, which achieves notable clarity and distinction in the use of the English in place of the Greek idiom. The translator has also avoided the pitfall of translating Aristotle's technical terms by those of modern biology so as to render the treatise pseudo-modern in style. A slip is the translation of *tetrapodon* as "fishes" (754a17); while the translation of *myria* as "heaps of others" is schoolboy slang; but these are rare and minor imperfections. There is a full outline of the contents of the treatise, and an index. As in all volumes of this series, Greek text and translation face one another.

As to the work itself, it might well take its place alongside the *Historia Animalium* in Raymond Pearl's *To Begin With* as required reading for all young biologists. In fact, of the two, the *Generation of Animals* is probably the more important, since here, as Dr. Peck has justly remarked, "Aristotle's thought is to be seen integrated as it is nowhere else; for in reproduction, as understood by Aristotle, not only the individual is concerned but the cosmos at large." The student should read it also for the numerous observations bearing on animal reproduction, heredity, and embryology, many of them amazingly accurate, many others erroneous or incomplete—one wonders, for example, whether Aristotle can ever have really seen insects in copulation. The student should also read it for the relation of fact to theory, as it is here that Aristotle achieved his most astonishing successes and made his most egregious blunders. His discernment of the epigenetic nature of development and the action of "principles" resembling hormones and morphogenetic movements in development was the product of the same logical processes of induction and deduction that led him to regard the determination of sex as due to the success or failure of the male "principle" in the semen to gain the mastery over the material (menstrual fluid) provided by the female, since the latter substance, if properly concocted, would develop into a male, but, with a deficiency of heat, would change over into the opposite condition and become female.

The wealth of material in the treatise is fascinating and well-nigh inexhaustible, and he who reads will find many a suggestion for experiment and observation even today. *Peri Zoion Geneseon* is no longer the Bible of biology, but it is indeed its genesis.

BENTLEY GLASS

THE RELIGIOUS AND PHILOSOPHICAL ASPECTS OF VAN HELMONT'S SCIENCE AND MEDICINE. *Supplement to the Bulletin of the History of Medicine, No. 2.*

By Walter Pagel. The Johns Hopkins Press, Baltimore. $1.00 (paper). ix + 44 pp. 1944.

Textbooks in the history of medicine, biology, and chemistry list a great number of fundamental scientific discoveries (introduction of the concept of gas, important insight into fermentation, digestion, metabolism, etc.) due to van Helmont (1577–1644) and omit a few more. The general opinion is that van Helmont made these discoveries in spite of his "queer" religious and philosophical opinions. Pagel has consistently opposed this psychologically and historically equally unfounded assumption since 1930, and he has shown that "van Helmont's biological bent is due to his religious zeal, and his scientific achievement the fruit of his religious conviction." "Religious motives led van Helmont (a) to scepticism towards human reason and (b) to empiricism as the way of truth and reality." As Pagel's earlier work is mostly written in German, it is most welcome to have now a short summary of his findings in English. This work has a larger significance than that of merely correcting errors concerning the individual scientist van Helmont, with whom the present small treatise deals perhaps too exclusively. It largely contributes to a better understanding of seventeenth century science and scientists in general. During the last fifteen years, we have learned (or relearned) that the primary motives of almost all great seventeenth century scientists were religious ones, and we will now have to look rather for those rare seventeenth century scientists who may have acted independently of such religious motivations.

To most biologists without historical training the book of Pagel will probably come as rather a shock. But it is perhaps not useless for them to learn that in scientific work, also, many ways may lead to the "Rome" of discovery and insight, and that after all the actual progress of scientific thought is a much more complicated thing than we are inclined to think on the basis of our own candor and the nice fables we are told in our youth.

ERWIN H. ACKERKNECHT

THE WOODS HOLE MARINE BIOLOGICAL LABORATORY. *By Frank R. Lillie. University of Chicago Press, Chicago.* $4.00. ix + 284 pp. 1944.

Many histories could and doubtless will be written about Woods Hole and its laboratories. Among them this volume will always occupy a special place because it alone is, as far as possible, an eyewitness account put on paper, "Before all those concerned with the early development of the Marine Biological Laboratory are gone . . . and it becomes too late to recapture the early enthusiasm that went into its making." The writing of this well illustrated, well printed, and well documented book by Frank Lillie (and E. G. Conklin, who collaborated generally and wrote certain sections) must have been a labor, but a labor of love.

These authors have succeeded in recapturing much of the "Woods Hole spirit," but they have done a great deal more. They have presented a highly informative and systematic account of the life history of a laboratory that is unique among institutions of its size and importance in being wholly controlled—peopled, administered, "trusteed"—by the scientific investigators who use it, and unique also in the extent of the role it has played in the development of biological research throughout the United States. The scope of this history extends from a time before Woods Hole was a a whaling port down to the 1940's.

Here the reader will discover many unfamiliar and sometimes curious facts about the founding and early activities of marine biological laboratories in both Europe and America. Here also he will find a photograph of the justly famous motto of the Penikese laboratory in Louis Agassiz's elegant copybook calligraphy, "Study nature not books," and the familiar picture of Agassiz lecturing at Penikese beside a blackboard covered with his diagrams of Radiates. The following pages describe the material and scientific growth of the Woods Hole Laboratory. Perhaps the most interesting feature is a series of eleven thumbnail sketches drawn around problems that formed centers of activity during the first twenty years. Including the investigators involved, it makes impressive reading: Animal Morphology, Descriptive Embryology, Experimental Embryology, Regeneration, Fertilization and Parthenogenesis, Cytology, Genetics and Evolution, General Physiology, Animal Tropisms and Behavior, Botany, the Medical Sciences. This parade is followed by a chapter portraying four early leaders, including Charles O. Whitman and Charles R. Crane.

The book ends with a sufficiently broad account of the social life of Woods Hole, the work and organization of the Woods Hole Oceanographic Institution, and finally an appendix of some seventy-six pages. Even in this last forbidding section the veriest outsider will find much that is rewarding imbedded in a frankly tedious matrix of committee reports, formal resolutions, and acts of incorporation. For it is there that he may see many of the actual wheels and cogs by which the laboratory has moved. The present generation of biologists may take heart from these fossil records of "battles long ago" that some supposed were but the inevitable death struggles of a laboratory run entirely by biologists.

This volume should have a useful function in interpreting the Woods Hole laboratories to the educated public. We know of few comparable books in which it is made as clear as it is here that scientific research depends for its ultimate support on an enlightened public.

G. B. MOMENT

A Source of Biological Names and Terms.

By Edmund C. Jaeger. Charles C. Thomas, Springfield and Baltimore. $3.50. xxvi + 256 pp. 1944.

This book is a carefully compiled, thorough, and easy-to-use guide to the etymology of technical terms in biology. It is essentially an alphabetical list of the stems or elements from which biological names and descriptive terms are compounded. Each stem is first cited; then the corresponding Greek, Latin, or modern word from which its use is derived; next the meaning or meanings; and finally, as examples, a number of technical words in which the stem appears, chosen to illustrate the various forms taken by the combining elements. By this arrangement the derivation and meaning of scientific terms are easily looked up and understood. A number of clear pen drawings lighten the appearance of the pages and serve to illustrate some of the characteristics and the resemblances, obvious or fanciful, upon which biologists have based their coinage of names. The list is said to contain 12,000 word-elements and to exceed by manyfold the scope of the unabridged dictionaries. Check of a few pages against one of the dictionaries fully corroborates this claim. Such a list cannot, of course, always explain a word fully without the parallel use of a dictionary. The choice both of terms listed and of examples refers primarily to descriptive zoölogy and botany, but many terms of mammalian anatomy, physiology, and medicine are included. In an excellent introduction, based in part on the preface of J. S. Palmer's *Index Generum Mammalium*, the author expounds the principles of scientific word-compounding and points out some of its puzzles and pitfalls.

Jaeger, who is a naturalist by profession, has based his philological work upon reliable sources and has obviously taken great pains to insure accuracy. The reviewer, after careful study, has noticed only one error, namely that under the stem *Trochant*— the anatomical term "trochanter" is wrongly defined, and the only cited meaning of the Greek word "*trochanter*" ("runner") is probably not quite relevant, for Josef Hyrtl, a great authority on such matters, thought that the process of the mammalian femur known by this term was named from a secondary use of the Greek word to designate the tiller of a boat. What few errors may be present in Jaeger's book are probably in special fields like this.

The book will be very useful to experienced biological writers and teachers; and for students it should be invaluable. Those who have a feeling for words and have studied classical languages will enjoy its use; those to whom etymology and terminology are obscure, burdensome, or vexatious matters will find in these pages a convenient source of help.

George W. Corner

Man and His Biological World.

By Frank Covert Jean, Ezra Clarence Harrah, and Fred Louis Herman, with the editorial collaboration of Samuel Ralph Powers. Ginn and Company, Boston. $3.50. viii + 631 pp. 1944.

This text for a college course in general biology is a revision of *Man and the Nature of His Biological World*, an earlier work by the same authors. The field surveyed is divided into nine units, dealing respectively with protoplasm and its metabolic activities; reproduction; nervous, hormonal, and other types of coordination and responsiveness; the nature and control of disease; the natural cycles; the balance of nature; evolution; genetics; and human cultural development. Most sections are clearly written, up to date, and errors are not numerous.

Exception must be taken, however, to the first chapter on genetic principles, which needs extensive revision and correction. The continuous spireme is still figured in mitosis; chromosome pairing in meiosis is said to take place as the chromosomes become arrayed at the equator of the spindle; the first meiotic division is described as purely reductional, the second as an ordinary mitosis; different symbols are used for alleles in discussing segregation and independent assortment in a highly confusing fashion; and there are numerous minor inaccuracies and unclear statements. The discussion of eugenic principles in a later chapter repeats some dubious conclusions. There is a tendency to preach: "Unworthy living, the excessive use of alcoholic liquors and drugs, or the contraction of venereal diseases on the part of the parents, may, through direct injury to the germ plasm, tragically blast and blight the health of the offspring throughout their whole lives." Perhaps the inheritance of acquired characteristics is not implied here, but freshmen will certainly be misled.

Another chapter that arouses criticism is the one on the present status of Darwinism. Natural selection is here treated in too narrow a sense. "For instance, it is maintained" by those criticizing the theory of natural selection "that many organisms have succeeded not so much by killing off less favorable variations as by possessing the characteristics that enabled them to succeed and multiply more abundantly in a given environment." The chapter then ends with a division of biologists into seemingly equal groups of those "who favor the purely selective position of Darwin and those who adhere to the idea of a more or less directed evolution." Authorities are arrayed on both sides, and the conclusion is reached, on the basis of Henry Fairfield Osborn's stand, that "we are more at a loss than ever before to understand the causes of evolution." In view of the availability of such excellent analyses of the causes of evolution as those by Dobzhansky, Haldane, and Julian Huxley, this is flatly antiquated.

Aside from these sections, the book may be recom-

mended. Illustrations are abundant and well chosen, but not always clearly reproduced or provided with adequate legends. There are questions for study and a list of references after each chapter, and a glossary and index at the end of the book.

BENTLEY GLASS

PAPERS ON ARCHAEOLOGY, ECOLOGY, ETHNOLOGY, HISTORY, PALEONTOLOGY, PHYSICS, AND PHYSIOLOGY. *Proceedings of the American Philosophical Society, Volume 87, Number 5.*

Various Authors. The American Philosophical Society, Philadelphia. $1.00 (paper). Pp. 365–460. 1944.

This number contains twelve papers, five of them being on biological subjects. "The Correspondence between Constantine Samuel Rafinesque and Thomas Jefferson," by Edwin M. Betts, is valuable for the light it throws on Rafinesque's work while at Transylvania University, on his devotion to science, and on his unavailing efforts to be appointed a professor at the newly founded University of Virginia. "The Earliest Account of the Association of Human Artifacts with Fossil Mammals in North America," by M. F. Ashley Montagu and C. Bernard Peterson, resurveys the purported discoveries by Albert Koch in 1839 of human artifacts associated with the remains of fossil mastodons and ground sloths, and establishes the high probability that Koch indeed made a genuine discovery, including that of the first Folsom point. G. H. Parker discusses "The Time Factor in Chromatophore Responses," and points out that, when a broad survey is made of animals showing melanophore changes, the evidence shows that nervous control is not always more rapid than hormonal control in producing a response. The dependence of both types of control on the mechanism of neurohumors is indicated. P. Lecomte du Nouy considers "Physiological Time" in a brief summary of ideas developed at length in his book *Biological Time*. Although not new, this essay is a proper rebuke to those who carried on the prolonged discussion of biological time in the columns of *Science* in 1944 without troubling to inform themselves of standard work on the subject. The longest of the five biological articles is "Studies on the Army-Ant Behavior Pattern.—Nomadism in the Swarm-Raider *Eciton burchelli*," by T. C. Schneirla. This is a full and very interesting account of the dependence of bivouac removal, in this species, on the development of intensive raiding during the day, on the decline of illumination in the afternoon, on traffic conditions, and on the "threshold of arousal" in the colony, but not on the scarcity or abundance of food in the vicinity of the community, as commonly supposed.

BENTLEY GLASS

STAIN TECHNIQUE.

By W. H. Emig. W. H. Emig, University of Pittsburgh. $1.00 (paper). 75 pp. 1941.

One can find in this handbook specific information about the properties and uses of 188 different biological stains, grouped under the headings of synthetic organic dyes (twenty-six classes), natural organic dyes, and inorganic coloring matters, and arranged in the order of their color index numbers. There are four brief general chapters. The second, on the chemical and physical properties of dyes, discusses color precipitates, reversible reactions, oxidations and reductions, and physical properties. The third, on the uses of stains, considers acid dyes, direct dyes, basic dyes, and dye nomenclature. The fourth discusses the principles of selecting contrasting stains for combinations. The whole manual represents an attempt to substitute a logical understanding of the uses of dyes, based upon their chemical and physical properties, for the pragmatic methods that at present so congest our handbooks and journals of microtechnique.

The discussions of the individual dyes give synonyms, type (acid, direct, basic, etc.), fastness to light, formula for solution, and some comments on uses in staining tissues, mainly those of plants. The chemical names and structures of the dyes, except in rare instances, are not given. That the handbook is not always accurate nor up to date is shown by the fact that it lists Janus green B, so useful in supravital staining, as obsolete; orcein, widely used for the giant dipteran salivary chromosomes and for elastic fibers, as principally an indicator; and basic fuchsin, used in Feulgen's specific stains for nucleic acid and glycogen, only as a stain for bacteria and vascular plant tissues. In spite of such faults and the inadequate basis at the present time for a complete treatment of the projected type, there is no doubt that this handbook will prove very useful.

ECOLOGY

UNBIDDEN HOUSE GUESTS.

By Hugo Hartnack. Hartnack Publishing Company, Tacoma. $12.00. 560 pp. 1943.

One is greatly impressed with the original manner in which this book has been written and compiled. It is not a textbook, yet it contains a world of factual information; it is not a novel, yet it holds one's interest and supplies genuine amusement. The author has apparently made every effort to enliven a subject that otherwise might prove boring to many. He has included interesting historical sidelights wherever possible and has dotted the pages with humorous cartoons that may or may not relate directly to the text material. The book covers a tremendous field, as evidenced by the fact that this is only the first of two volumes to

be published. "An unbidden house guest" is considered to be any undesirable plant or animal that ventures on or within a dwelling. The scope of the material is still broader, since some of these house pests bring with them other plants and animals that cause human disease. To be a bit facetious, in view of the completeness of the book, one cannot help but wonder if the author will discuss in his second volume how to rid the house of other specimens of *Homo sapiens* who are no longer welcome.

The author came to the United States from Germany in 1924. From his experience as a pest control operator, he has observed a need here in America for a book informing various groups about the habits of pests and the ways of controlling them. Although his background has made it practically impossible to eliminate all Germanisms from his style, it has made it possible for him to furnish his English readers with valuable information obtained from the literature of his native country. Apparently this extensive source of information has been largely overlooked by workers in this country. The freshness of his book is due to a great extent to the reproductions of many excellent illustrations from European publications.

After a lengthy introductory section, he takes up the plant and animal kingdoms in an orderly manner and discusses the pests, parasites, and micro-organisms that belong to each of the major phyla, classes, and orders. The one notable omission is that of the true insects, which are to be presented in the second volume.

It is unfortunate that the sale of this book has been restricted to 1500 copies. Although it has been written specifically for pest control operators, contractors, and others interested in offering protection against house pests, it should be helpful to medical zoologists, public health workers, and students of hygiene. It would be a worthwhile addition to any high school or college library, for even if not studied, much general information can be obtained by even a casual scanning.

More than likely this individualistic book will please some and provoke others. While it contains a great deal of information, its organization may to a certain extent reduce its usefulness. There are five sections to the book, each having its own table of contents and sequence of page numbers. There is no general table of contents at the beginning of the book to direct the reader to the various sections. Furthermore, there are titles to the last four sections and none for the first. The reader must note the items listed in its table of contents in order to ascertain that the first section of 226 pages deals with general information regarding house pests and methods of control. The long index could have been improved if the page numbers had been given more often, instead of references to a more general heading that is often an unfamiliar scientific name of an organism. These features of the book that were found objectionable to the reviewer should not detract too much from its fundamental value. They are nearly all editorial faults that could have been easily corrected by someone experienced in organizing such material.

M. M. BROOKE

GENETICS AND CYTOLOGY

MITOSIS: *The Movements of Chromosomes in Cell Division. Columbia Biological Series Number XIV.* *By Franz Schrader. Columbia University Press, New York.* $2.00. x + 110 pp. 1944.

Mitosis is the ultimate basis of heredity, and the discovery of the forces and mechanisms involved in it is one of the great problems of biology. From the discovery of the chromosomes and the spindle mechanism to the present day, cytologists have not ceased to elaborate hypotheses about the nature of chromosome movements. Yet at the present time, says the author of this monograph, "not one of the many hypotheses that have been broached has in it the definite promise of a final solution. But we have come to realize that mitosis is comprised of a great complex of different mechanisms."

Schrader has produced a survey of present knowledge of the subject of chromosome movements in mitosis that is comprehensive and well balanced, although brief and selective rather than exhaustive in treatment. He has deliberately excluded the reconsideration of work antedating the present half century, and also that summarized in an adequate fashion elsewhere. Although this has saved much space, it has not always worked to advantage. Thus the young student might be misled as to the validity of the electrostatic theories if he failed to consult Wilson's discussion of the subject in *The Cell in Heredity and Development*. The difficulties presented to any such hypotheses by tripolar spindles and the diagonal spindles in quadripolar figures, although still crucial, are not considered in Schrader's monograph. It is only fair to point out that Schrader is careful to make the necessary references, but why Lillie's hypothesis should receive such prominence when the objections to it are left to references is not clear. One wonders whether all the cytologists who have continued to develop new versions of the electrostatic hypothesis have been aware of the fundamental objections to it.

The brief introduction is followed by a chapter on the structural elements involved in mitosis. Evidence from living as well as preserved cells, from unusual and abnormal as well as from normal ones is focussed on the questions of the reality and nature of centrioles, spindle fibers, kinetochores, asters, and spindle constituents. The recognition of two principal types of spindle is in agreement with the views of Bleier, Belar, and others, although the views of Belar on the distinction between the nuclear and cytoplasmic (or "central") components

of the spindle are not discussed. The continuous fibers are regarded as cytoplasmic in origin by Schrader, and the chromosomal fibers as nuclear, perhaps, like the interzonal connections, chromosomal. The evidence for the homology of centrioles and kinetochores is also presented.

In the end, none of the hypotheses are satisfactory, although several—contraction and expansion of parts of the spindle, electrical charges, chromosome autonomy, tactoids, etc.—may contain elements of the larger truth. Most of these hypotheses have concerned themselves with metaphase and anaphase movements, and even now we are unable to relate interphase and prophase behavior to what follows later.

In the chapter on related problems, meiotic behavior, telomere attractions, heteropycnosis, and other phenomena are considered. It is here that the monograph seems most curtailed, for while the meiotic mitoses are by no means ignored, the survey can hardly be said to review the extensive subject of chromosome pairing and the role of chiasmata. This is to be regretted, since we would not only like to have Schrader's careful analysis of it and his views about it, but also because of the suspicion that the behavior of the chromosomes in synapsis and crossing over cannot be altogether foreign to their behavior in regular mitosis. If, as Schrader suggests, the most hopeful attack upon the problem may well be that of concentrating on some one phase of the cycle, in favorable material, it might very well be some aspect of the meiotic prophase that would yield the first success.

BENTLEY GLASS

MEDICAL GENETICS AND EUGENICS.

By Charles B. Davenport, Clyde E. Keeler, Maude Slye, and Madge Thurlow Macklin. Woman's Medical College of Pennsylvania, Philadelphia $1.00. 141 pp. 1940.

This slender volume contains a series of lectures on human heredity delivered at the Woman's Medical College of Pennsylvania in 1940. While geneticists will welcome the signs of growing interest in heredity on the part of American medical schools, these lectures are certainly of very unequal merit, and the lean kine may have eaten up the fat ones. The first three lectures were given by Davenport. In his first, he discusses human variability in physical and mental traits. While recognizing the force of both genetic and environmental factors, Davenport relies chiefly on family pedigrees for demonstrating the role of the former and may be charged with failure to discern the importance of common family influences, education, and social and economic background in molding individual interests and temperament. To say the least, a pedigree lumping incest, epilepsy, feeblemindedness, criminalistic tendencies, and alcoholism has dubious *genetic* significance. Moreover, the pedigrees extend back one or more centuries, cannot be regarded as complete, and certainly depend in most instances on evidence that any critical person would have to reject as unreliable. Just what the pedigrees of notable naval families illustrate, other than the effect of social acceptability on marriage and the effect of family tradition on the choice of a career, it is hard to see.

In the second lecture, there is more of the same—together with an attack on the principle of democratic equality, an attack based on the grounds of the genetic dissimilarity of individuals. But the fortunate diversity of genetic potentialities in human beings emphasized by Davenport was most certainly as evident in the eighteenth century as now, and was indeed at the root of the democratic doctrine of equality of opportunity that has characterized America. If the doctrine of equality has any meaning whatever, it means the equal right of each individual, regardless of color, creed, or nobility of pedigree, to "make the most of himself." Genetic diversity is thus recognized and made the chief pillar of that concern for human individuality and that tolerance of other's differences which characterize true democracy.

Davenport's third contribution is less subject to criticism, its errors being of a more technical nature. His emphasis upon the importance of the genetic constitution in the incidence of disease is certainly well placed. The story he tells of research on mouse leukemia affords an excellent example of what is supposed to be a pathological entity proving upon genetic analysis to comprise a number of diseases. But the statement that hemophilia is "carried in eggs only" is a gross error in describing sex linkage, and the attribution of maternal influence in leukemia "obviously" to the cytoplasm ignores the probable effects of uterine environment or a milk factor.

Keeler contributes a discussion of genes in chemical terms, of gene action in development, and of the meaning of evolution in terms of genes, pointing out the similarity of gene constellations in different mammalian species and the significance of parallel mutation, with the aim of showing why mutants in laboratory mammals are such valuable materials for the study of medical genetics.

Maud Slye, in a concise and excellent account, sums up her work on the incidence of cancer in different genetic strains of mice, presenting evidence for the genetic control of the type of malignancy, of the site of malignancy, and of the age at which malignancy will occur.

The final lecture is by Madge Macklin. In graphic fashion she tells about instances in which an ignorance of genetic knowledge led to medical mistreatment or in which such knowledge pointed the way to correct treatment or advice. She concludes by emphasizing that inherited diseases are not thereby incurable, and that we must have adequate courses of medical genetics in

medical schools, as well as centers of research in this most neglected field.

BENTLEY GLASS

MEDICAL GENETICS AND EUGENICS. *Volume 2.* *By R. Ruggles Gates, Laurence H. Snyder, and Earnest A. Hooton. Woman's Medical College of Pennsylvania, Philadelphia.* $1.00. 60 pp. 1943.

This second series of lectures on medical genetics to students of the Woman's Medical College of Pennsylvania includes three addresses, given in 1941–1943. In the first lecture (13 pp.), Gates makes a general introductory survey of human evolution, followed by a discussion of the heredity of racial differences and the description of some human hereditary abnormalities of medical interest. Gates is mistaken in saying that a fossil series can be traced from *Australopithecus* through *Plesianthropus* and *Paranthropus* to Rhodesian man, since these South African apes were Pleistocene contemporaries of each other and of man himself.

In the second lecture, Snyder outlines succinctly the practical applications of a knowledge of human heredity in the field of medicine. He discusses instances of autosomal, sex-linked, holandric, and partially sex-linked genes and presents a genetic map of the human sex chromosomes. Linkage, penetrance, expressivity, viability, ontogenetic relations, and gene frequency are other topics considered. One can only wish that this discussion might have been greatly amplified.

The lecture by Hooton emphasizes the universal basis of heredity in physical, mental, and pathological conditions. Hooton overstates his case and underestimates the role of environmental factors. Every "familial" condition appears to him necessarily hereditary, although the story of pellagra makes it sufficiently obvious that families have other common bases, besides genes, for developing common characteristics. Hooton expresses a belief in orthogenesis, yet the gist of his thought seems to be that "some adequate substitute must be found for the obsolete forces of natural selection which in times past have sifted out the inferior human stuff." This he sees in the knowledge and application of human genetics, once geneticists have overcome their "pusillanimity" and doctors their preoccupation with other things. Hooton feels that premedical education should receive a change of emphasis from chemistry and histology to vertebrate comparative anatomy, genetics, physical anthropology, and biometric statistics, and many of us will agree with him on this point. But were he more widely acquainted with genetic work, he would hardly regard the interesting work of W. H. Brown *et al.* on constitutional types and disease proclivities in rabbits as a piece of research *sui generis*. Hooton likes to gibe, to prophesy, to speak *ex cathedra*. One quotation is illustrative and pertinent in present times: "There is but one way to insure peace and that is to extirpate all predacious men and to raise the level of intelligence in human masses to a height where it will no longer be suggestible to the leadership of paranoids and others who lust for power." As a counteractant for this sort of reasoning, one should reread Weinstein's essay *Palamedes*.

BENTLEY GLASS

GENERAL AND SYSTEMATIC BOTANY

THE MYCETOZOA OF NORTH AMERICA. *Based upon the Specimens in the Herbarium of the New York Botanical Garden.* *By Robert Hagelstein. Published by the author, Mineola, N. Y.* $6.00. 306 pp. + 16 plates. 1944.

In this compact volume are descriptions of 285 species reported from North America and considered valid by the author, 269 of these having been studied from the representative specimens from North America in the herbarium of the New York Botanical Garden, while at least 216 were also studied by the author in the field and in the laboratory from his own collections and those of his colleagues covering the territory from Quebec to Florida. It is therefore a thoroughly adequate representation of the 318 species that the author considers valid of the total number which have been reported for the world. As would be expected, this authoritative presentation is the result of long continued and thorough investigation. This group for more than twenty years has been the absorbing interest of the author who, in his capacity as honorary Curator of Myxomycetes at the New York Botanical Garden, has had access to the wealth of authentic material from the large original collections of J. B. Ellis and W. C. Sturgis, as well as the thousands of additional specimens received by exchange and donation from correspondents, augmented by the best of the more than 10,000 collections made by the author and by the associates and friends whom his infectious enthusiasm and sincere interest have inspired as collaborators.

After a preface of two pages outlining the background of the work, the introduction discusses the characteristics, nature, method of development, habitats, and occurrence of the Myxomycetes, with methods of collection and study and the bases of classification. There is also a helpful glossary for those to whom the technical terms used in this somewhat specialized group may be unfamiliar. The outline of families and genera follows the accepted classification scheme developed by Lister.

The discussion and description of the genera and species in 258 pages forms the main body of the book. This descriptive treatment is supported by 16 plates, a frontispiece showing the woodland habitats ideal for collecting, while four plates in color from Sturgis' drawings excellently portray the habit of five species especially critical or interesting, as well as the microscopic charac-

ters of their spores and capillitium. The remaining plates, 6 through 16, are half-tones of representative fruiting bodies magnified from three to nine times to show their distinctive features. The plates are excellent, the only possible criticism being that there are so few illustrations of the microscopic characteristics of spores, elaters, and capillitia. There are, however, two excellent figures of the characteristic plasmodia. In general the plates are valuable, well chosen, excellently reproduced. The explanations of some of the plates offer more than the usual brief descriptive captions, since they correct errors in the magnification of certain plates by Sturgis when previously published, furnish descriptions for maintaining plasmodia for study, and give the characteristic colors of the specimens photographed.

In the conclusion the author compares the impressive assemblage of forms presented here with those known from other parts of the world and briefly discusses synonymy, distribution, and other general matters of biologic interest.

The extensive and useful five-page list of the literature cited or consulted, prepared by J. H. Barnhart, the Bibliographer Emeritus of the New York Botanical Garden, is appropriately restricted to the taxonomic literature.

The useful index to genera and species lists the accepted names in bold face and the synonyms in italics, while asterisks denote the 33 species not known from North America, as listed on page 274.

The book is an authoritative and complete monographic treatment, a worthy successor to the earlier works of Lister and of MacBride.

In addition to the technical taxonomic descriptive material, there is a wealth of material of general biologic interest. The number of genera with but single species, ranging from *Alwisia* through *Reticularia*, 21 in all, present an interesting contrast to the ten or a dozen genera which have ten to twenty species each, with *Physarum*, as always, far surpassing all others with its total of 62. Speculation as to biologic reasons for the high proportion of monotypic genera in this apparently ancient group would be of interest.

As might be expected, according to the Age and Area Hypothesis, a notable lack of endemism is obvious in this group. There are numerous cases in which the type locality was Java, Ceylon, Tasmania, Paraguay, or similar remote or isolated localities, yet subsequent collections have shown the species to be common in North America and Europe, or even of world wide distribution.

The favorite substrata, dead wood, leaves, and the like, predominate, indicating a notable lack of specialization, since certainly these substrata in Java are not of the same precise composition as the dead wood on which the species appear in the United States. There are also interesting cases of more restricted habitat, the rare *Lachnobolus congestus* having been found twice on old sugar bags. The restriction in substratum shown by *Craterium concinnum*, which, so far as is known, occurs in eastern North America only on decaying chestnut burs of the preceding year and hence has been found only rarely since the chestnut blight almost completely exterminated the sources of such material, and shown by the companion species *Arcyria globosa*, which is found chiefly on chestnut burs but may also occur on weathered leaves of the not too closely related chestnut oak, suggests interesting possibilities of the extinction of similarly restricted species in the past through the extermination of the substratal sources by epidemics.

There is also ample evidence that even in this group, world-wide in distribution and intensively studied, there is still opportunity for the discovery of new and interesting species in woodlots in one's own vicinity.

It is to be hoped that even though one phase of the author's work is completed with the publication of this able book, he will still continue for many years to enrich our literature through further studies of this fascinating and biologically significant group.

WM. H. WESTON

MUSHROOMS OF THE GREAT LAKES REGION. *The Fleshy, Leathery, and Woody Fungi of Illinois, Indiana, Ohio, and the Southern Half of Wisconsin and of Michigan. By Verne Ovid Graham. The Chicago Academy of Sciences and The Chicago Natural History Museum. Chicago.* $4.10 (paper). vii + 390 pp.; 49 plates. 1944.

The author, Honorary Curator of Mycology at the Chicago Academy of Science, conceived the idea of preparing this manual in 1927 when, while giving a course on the fleshy and woody fungi at the University of Chicago, he found it necessary to assemble the publications dealing with those of that region. The present volume, covering the fleshy, leathery, and woody fungi of Illinois, Indiana, Ohio, and the southern half of Wisconsin and Michigan, includes around 1200 species, thus extending not only the scope but also the geographic range of Moffatt's *Higher Fungi of the Chicago Region*, which appeared in 1909 and 1923 and included 400 species.

After a brief three-page preface giving the background of the book and explaining the nature and activities of fungi, there follows a ten-page key to the genera. This key, of the conventional dichotomous type, will probably present unexpected difficulties to the beginner and, since it necessarily employs numerous technical terms, will require support from the dictionary of terms on pages 366 to 370, from plate 1 with its diagrams of various types of fungi, plate 49 with its illustrated glossary of the shapes of pilei, stipes, gills,

and other morphological features, and plate 12 with its illustrations of the types of fruiting bodies of the Agaricaceae.

The Ascomycetes are next covered in 29 pages, the five families discussed comprising the more conspicuous forms commonly encountered. The Basidiomycetes, as is natural, occupy the greater part of the book (about 320 pages), and are taken up by families, excluding of course the rusts, smuts, and other forms which do not fall in the category of conspicuous leathery, woody, or fleshy fungi. An index of 17 pages furnishes adequate reference to the genera and species, with helpful inclusion of references to the figures illustrating each. The illustrations, plates 1–49, assembled at the end of the book, comprise collotype reproductions printed at the collotype plant of the museum from figures executed by members of the WPA working from the author's original drawings, from selected photographs, and from specimens in the E. T. Harper collection at the Chicago Natural History Museum. These illustrations, which should be the most effective portion of a book of this type, are in general disappointing. Some are very excellent, others are rather crude and highly diagrammatic and seriously fail to exploit the notable potentialities of collotype as an exquisite medium for the reproduction of scientific material. In general there is a serious lack of the structural details essential to identification. To be sure, in figures 24 and 29 of plate 5 two types of basidia are shown, while in figure 7 there is an attempt to show something of the structural characters of *Hymenochaete*, but these are of little worth in helping the reader visualize numerous essential structural features. The lack of detailed illustrations of the spore characteristics of such genera as *Lamprospora* among the Ascomycetes or *Russula* among the Basidiomycetes, where spore characters are highly significant in diagnosis, greatly curtails the usefulness of the book. To be sure, in plate 40, the illustrations of the fruiting bodies of various species of *Inocybe* are accompanied by drop-like objects presumably meant to be spores, but their vague, uncertain sculpturing and the lack of explanation nullify their usefulness. The plates lack any detailed explanations that might help to supplement their inadequacy and render them more serviceable, the illustrations, in most cases, being merely named without any helpful indication of the distinctive characteristics or structural features significant in identification. The almost complete lack of scales of magnification or reduction is inexcusable; the few that are given increase rather than lessen the confusion.

The book is neither an adequate popular handbook for the use of the interested amateur nor an authoritative regional monograph for the mycologist. For the amateur, although it includes a wider range of fungi, it will by no means prove as useful as the excellent handbooks of Gussow and Odell or of W. S. Thomas. For the mycologist, while it does present under each family a few references to the pertinent monographic literature with occasional references under genera, in general it shows a lamentable lack of the features that are essential to a dependable scientific treatment of any group. One gains the impression that this book cannot be depended upon for sound nomenclature, acceptable treatment of synonymy, or authoritative identification of difficult specimens.

WM. H. WESTON

THE FLOWERING PLANTS AND FERNS OF MOUNT DIABLO, CALIFORNIA: *Their Distribution and Association into Plant Communities.*

By Mary L. Bowerman. The Gillick Press, Berkeley. $3.75. xi + 290 pp. 1944.

Notable productive activity in the field of botany in California has manifested itself in the excellent monographs, floras, and manuals which have appeared in recent years. To these this book is a useful addition, for it presents an intensive phytogeographical and ecological study of an area distinctive in topography, climate, and soils. The author's work, begun in 1930 and carried on intensively through 1935, led to her doctorate thesis at the University of California in 1936 and with continued work since then has now developed into this book. The stimulating and guiding influence of W. L. Jepson, justly famous for his pioneer investigations and long continued study of the flora of California, is shown throughout.

Mount Diablo, lying thirty miles east northeast of San Francisco, is an isolated peak 3849 feet high, well suited for this intensive study. The area covered includes 550 square miles, in which the climate is in a borderline between the cool summer and the hot summer type and the life zone ranges from the Sonoran to the transitional. The illustrations, comprising 26 figures, some line cuts of maps, curves of rainfall, etc., but mostly excellent half-tone reproductions of photographs, vividly portray the diversity of the terrain and the rich opportunities for intensive botanical work.

After considering the physical factors, such as position, topography, climate, soils, and geology with a brief but significant discussion of the paleobotany, the vegetation is studied in detail in Part Two, each of the several formations with its subsidiary associations being adequately discussed, from the broad sclerophyll formation and the deciduous oak conifer formation through the riparian formation of the canyons and gulleys and the formations of the grasslands, the chaparrals, the springs, and the ponds. There follows an interesting and interpretive treatment of the successions which can be traced in the woodland, the grassland, and the chaparrals, with a brief but effective discussion of the effect of fire.

After a brief treatment of the correlation between

the vegetation, the soils, and the geology of the region, there follows a highly significant analysis of the content and relationship of the flora. Here the vascular plants of Mount Diablo are shown to comprise 630 species in 83 families, the seed plants comprising most of these with 525 native species, 6 of which are endemics, and 91 that have been introduced mostly from the Mediterranean region of Europe, while the ferns and their allies have a small representation of 14 species and three families. This flora is analysed by altitude, the ranges of its component plants are compared, their origins are discussed, their relation to the character of the terrain, to soil types, and to methods of seed dispersal are noted, and the nature and distribution of the alien elements are examined.

There is a discussion of the collections from the early random gatherings that began with those of the pioneer Brewer in 1861, through the beginnings of more intensive study by Jepson and others from the 1890s, to the more recent work, especially the intensive and comprehensive studies and collections of the author.

The main body of the book presents an annotated catalog of the vascular plants in 176 pages, beginning with an eight-page key to the families or genera, covering the Pteridophytes in four pages, and taking up the families of the Spermatophytes from the Pinaceae to the Compositae in the remaining 172 pages. In this catalog the habitat, associated plants, and specific localities are given for each species, with listings in the order of dominance in the association. Since this treatment is that of a catalog list rather than the descriptive listing of a manual, those not familiar with the species concerned will need Jepson's *Manual of the Flowering Plants of California* or his *Flora of California* to discover the characteristics of the individual species concerned. The plants are quite fittingly considered as components of associations and representatives of localities rather than as botanical entities, although considerable data as to their characteristics may be derived from the keys.

There is a helpful five-page list of literature cited and an adequate four-page glossary of the terms used in the keys, while the index presents both the common and scientific names of the species, genera, and families, thus facilitating ready reference.

All in all, this is a complete, thorough, and vivid picture of the ecology and botany of a distinctive mountain region, and will prove of great value not only to botanists of the vicinity but to those making similar studies of the flora of comparable mountains elsewhere.

WM. H. WESTON

FLORA OF TEXAS. *Volume 3, Part II. Anacardiaceae, Cyrillaceae, Aquifoliaceae Genus Cuscuta, Convolvulaceae. Volume 3, Part III. Orchidaceae. By Cyrus Longworth Lundell and Collaborators. University Press in Dallas, Southern Methodist University, Dallas.* Vol. 3, Pt. II, $1.50 (paper); Vol. 3, Pt. III, $3.00 (paper). Pp. 89–150; 151–196 + 34 plates. 1943; 1944.

These two parts follow Part I which, in the first 88 pages of Volume Three, presented Harold N. Moldenke's Eriocaulaceae, Avicenniaceae, Verbenaceae issued in June, 1942. They are a continuation of the flora sponsored jointly by the Southern Methodist University and the University of Michigan Herbarium under the leadership of Lundell, using as collaborators various botanists who are authorities in the taxonomy of the several groups. They follow the laudable plan of presenting descriptions of all the ferns and flowering plants which grow naturally within the state. Of the ten volumes planned, the first and second will give the general discussion of the background of botanical exploration of the state, with keys to families and a complete catalog of the species, while Volumes Three through Ten, devoted to the descriptive flora by families or genera, will be published as parts like these.

Following this plan the Anacardiaceae are ably presented by Barkley of Montana State University, Lundell covers the two species which represent the Cyrillaceae and the ten species of Ilex which represent the Aquifoliaceae, while Yuncker of De Pauw University contributes an effective descriptive treatment, with diagrams of the floral parts essential for the identification, of the 24 species of *Cuscuta* occurring in the state.

Correll's presentation of the 15 genera and numerous species which represent the Orchidaceae in Texas is highly satisfactory. The author's own knowledge of the group, the resources of the Oakes Ames' Herbarium of the Harvard Botanical Museum, and especially the artistically beautiful and scientifically accurate plates, chiefly by Mrs. Ames, with a few by Dillon, combine to form an unusually effective descriptive treatment of the family.

There has in this country been just criticism of the "Fascicle racket" so ably exploited by our European colleagues; libraries and other institutions committed to subscription pay under this instalment system a disproportionately high total price. Similar criticism might perhaps be advanced here, for while many institutions secure this series by exchange, others who pay the set price have already spent $6.00 for the 196 pages that have appeared, leading one to believe that the total for the ten volumes will be high in comparison with such floras as Jepson's for California or Abram's even more comprehensive *Flora of the Pacific States*. The advantages of the system, of course, are the immediate usefulness of the separate parts as issued, without the long wait necessary before such an ambitious and comprehensive work is completed in its entirety.

In any case the appearance of additional parts of this flora will be awaited with interest.

WM. H. WESTON

JOHN MERLE COULTER. *Missionary in Science.* *By Andrew Denny Rodgers III. Princeton University Press, Princeton.* $3.75. viii + 321 pp. 1944. This is an admirable book—a thorough and appreciative biography of one of the great figures in American Botany, a searching and interpretative history of the significant scientific era in which he played an important part.

Here Coulter's life is portrayed from his birth on November 20, 1851, in China, where his father was serving as superintendent of the Mission Press at Ningpo, to his death on December 23, 1928, only five days before the testimonial meeting arranged by the Botanical Society of America to honor him for his many years of leadership and outstanding service in the field of botany. The early influences which shaped him are traced in the first chapter, covering the years at Hanover College in Indiana, from his preliminary training in the Preparatory Department, which he entered at thirteen, to his graduation in 1870 with a thorough background in religion and the classics and an appreciation of the natural sciences; while the next chapter follows his field work as assistant geologist in Utah under Frank H. Bradley in the geologic and geographical survey of the territories in 1872, and his later work in the Hayden Expedition in Colorado, field work which crystallized his intense interest in botany. The account of his early years of teaching at Hanover is illuminating and sympathetic in its portrayal of his youthful limitations and of his energy and courage in starting the Indiana flora and founding in 1875 the Botanical Bulletin, which from 1876, as the Botanical Gazette, kept pace with the development of botany until in 1896, when taken over by the University of Chicago, it had become a leader in its field.

With notable grasp of the subject and understanding of the man, the author traces Coulter's growth to pre-eminence: the Rose professorship of geology and natural history at Wabash College beginning in 1879, with stimulating periods of summer work in 1879 and 1880 at Harvard with Asa Gray, Goodale, Farlowe and others; the presidency of Indiana University in 1891, and of Lake Forest College in 1893; the appointments at the University of Chicago as professorial lecturer in Botany in 1894, and as Professor of Botany in 1896, with the productive years of leadership that ensued until, in 1925, at the age of seventy-four, he retired from teaching to become chief scientific adviser to the Boyce Thompson Institute.

The reasons for Coulter's pre-eminence are well brought out; in him were blended unusual ability as an investigator, an organizer, and a leader; he was a man of vision who grasped and interpreted principles; he was quick to see opportunities for the development of research, was alert to sense developmental trends in the rapidly growing field of botany.

From Coulter as its central figure this historical account extends to such other outstanding contemporaries as Bessey and Farlow, tracing their activities and influences as they interacted with those of Coulter, and showing how the impetus and stimulus of all these pioneers were transmitted and multiplied in the younger men of the rising generations trained and influenced by them.

Even the index of this book is an impressive roster of the botanists and other scientists of the period from 1870 to 1928, an indication of the competency with which this book reflects the personalities, the institutions, the societies, the meetings, the surveys, the publications, the herbaria—all the many aspects of the living and rapidly developing period of science in which Coulter played so prominent a part.

The author is to be congratulated on his success as a biographer, but even more on the grasp, perception, and insight with which, as a scientific historian, he has caught the spirit pervading botany in this active period, the personalities and ideals of the contributing botanists, and the nature of the problems and trends in this era of which they were a part.

The book is a vivid cross-section of the rapid development of botany in America, a development in which Coulter played a leading part. It is eloquent evidence that botany has found in the author a spokesman and historian, and an interpreter of the significance of botanical investigation and of its contribution to the material as well as the scientific progress of a period. It is much to be hoped that the author will continue developing in detail the history of the growth of botany in the United States. With the present volume as convincing evidence of his unusual capability as a biographer and an interpreter, his forthcoming book, *American Botany, 1873 to 1892: Decades of Transition,* will be awaited with eager anticipation not only by botanists but by scientists and historians as well.

WM. H. WESTON

PARASITOLOGY

THE PARASITES OF MAN *in Temperate Climates. Revised.* *By Thomas W. M. Cameron. The University of Toronto Press, Toronto.* $3.00. xi + 182 pp. 1942. As the title indicates, this book is concerned with those parasites of man that are found in temperate climates, primarily those of North America and Great Britain. Exotic parasites are barely mentioned or are omitted entirely. For example, the following are some of those that are not included: *Trypanosoma gambiense* and *rhodesiense*, all of the leishmanias, *Fasciolopsis buskii*, and all of the filarial worms save *Wuchereria bancrofti*. However, quite a number of indigenous organisms that are potential human parasites are discussed: *Apophallus venustus, Dicrocoelium dentriticum, Metorchis conjunctum, Parametorchis complexus,* and *Opisthorchis*

pseudo-felineus. It is stated in the preface that the book is intended for the practitioner and not for students of tropical medicine, parasitologists, or laboratory workers. In view of the service men returning from the present world conflict, it might be expected that practitioners here at home will be just as likely to encounter one of the known exotic human parasites as one of the potential parasites.

Aside from the above possible criticism, the book definitely fills the need for a textbook that emphasizes the human parasites of temperate climates. Fortunately it is written by a recognized authority on the subject, the Professor of Parasitology at McGill University and Director of the Institute of Parasitology of Macdonald College, Quebec, Canada. One is particularly impressed with the clear concise manner in which the author presents detailed information and fundamental parasitological principles to the reader. For instance, the following is an example of this ability: "The conditions under which helminths cause disease are quite different from those of the protozoa. As with them, however, disease almost always results from numbers, but unlike them, these numbers must all enter from the outside of the host. Thus while a single amoeba may ultimately cause amoebic dysentery, a single hookworm will never cause clinical disease."

Although this book is no doubt written specifically for the author's course in parasitology at McGill University, it might prove suitable for many other similar courses given in temperate climates. The instructor should of course realize the restricted scope of the text and should have more complete reference books available for the student. There are 61 well selected illustrations, a bibliography, and an index.

M. M. BROOKE

THE CONTROL OF BILHARZIA IN SOUTHERN RHODESIA. *By Alan Moxley. Salisbury, Southern Rhodesia.* 307 pp. 1944.

A debilitating disease that man is subject to over more than one half of the world is caused by a small worm, *Schistosoma*, and so the disease is called schistomiasis, or bilharzia. In Southern Rhodesia there are two species of *Schistosoma* that infest the blood vessels of man, one found in the intestine and the other in the urinary organs. They enter through the skin, and after some months lay eggs that pass out into water, where they hatch as microscopic embryos that enter snails, each species entering only one of two species of snail. After a few weeks in the snail host, the worms return to the water and perish, within a few days, unless they manage to enter man through his skin.

The author of this book is a malacologist with wide knowledge of water snails in America, Europe, Siberia, and Africa, who went out to Southern Rhodesia with the director of the Ross Institute of Tropical Hygiene, London, to find out what should be done to check this disease that afflicts 35 per cent of the natives and 8 per cent of the Europeans and in some spots up to 90 per cent of the natives. Through 1939 to 1942 thousands of pools and water courses were examined and snails experimented with in a laboratory built for this research. The conclusion was that while the parasite can be killed in man or in the water or in the snails, the best way is to kill the two species of water snail that are necessary secondary hosts for the parasites on their journey from man back to man.

Many experiments made with inorganic and organic substances showed that some would kill the snails without danger to man. Among the plants effective were Eucalyptus, *Tephrosia vogelii* and *Swartzia madagascariensis*. Of this last the pods contain up to 20 per cent saponins (glucosides). But in addition to these substances excellent results were obtained with malachite, which contains copper carbonate and kills the snails when in very weak doses.

Explicit directions for the preparation and scattering of these killing agents are given, along with valuable suggestions for local problems. The natives use some of these plants to kill fish, and posters in their languages urge them to combat the disease with these leaves, and with the malachite they are to obtain from the Government. With native aid the Government may be able to stop the spread of the disease and eliminate it in some localities, and may hope to eradicate the disease eventually.

E. A. ANDREWS

PARASITIC COPEPODS IN THE UNITED STATES NATIONAL MUSEUM. *Proceedings of the United States National Museum Volume 94, Number 3177.*

By Charles Branch Wilson. Smithsonian Institution, United States National Museum, Washington. Paper. Pp. 529–582 + plates 20–34. 1944.

A report completing the identification and description of all parasitic copepods in the United States National Museum. Fourteen new species, six new genera, and the undescribed sex of six other species are described; one new variety, one renamed species, and fourteen other species are also included.

THE ARGASIDAE OF NORTH AMERICA, CENTRAL AMERICA AND CUBA. *The American Midland Naturalist Monograph No. 1.*

By R. A. Cooley and Glen M. Kohls. The University Press, Notre Dame, Indiana. $2.00. 152 pp. 1944.

This first monograph of the American Midland Naturalist is concerned with the soft ticks of the northern and central portions of the Western Hemisphere. It is written by two entomologists of the Rocky Mountain

Laboratory (U.S.P.H.S.) who are authorities on the taxonomy of ticks.

Brief introductory sections are devoted to statements on the medical and veterinary importance of the soft ticks, explanation of morphological terms, and descriptions of techniques for examining ticks. The authors accept four genera in the family Argasidae: *Argas* Latreille 1795, *Ornithodoros* Koch 1844, *Otobius* Banks 1912, and *Antricola* Cooley and Kohls 1942. They present detailed morphological descriptions of the species of these genera that are found in the regions covered by the monograph. The text is illustrated by line drawings and photographs. Spot maps assist in designating the geographical distribution of the species. In all, there are seventy-one drawings, maps and photographs. At the end of the book are lists of the ticks according to their known hosts and distribution in Canada, United States, Mexico, Guatemala, Panama, and Cuba. An extensive bibliography and an index are included.

MOSQUITO CONTROL: *Practical Methods for Abatement of Disease Vectors and Pests. Second Edition.*

By William Broadbeck Herms and Harold Farnsworth Gray. The Commonwealth Fund, New York. $3.50. xiv + 419 pp. 1944.

All of those engaged in mosquito abatement and malaria control are acquainted with this handbook of Herms and Gray. The enthusiasm with which it has been received is apparent from the four printings of the first edition since it first appeared in 1940. This present second edition, which has been greatly enlarged and brought up to date, will no doubt prove to be even more useful.

The first hundred or more pages deal with fundamental considerations of problems of mosquito control, such as its economic importance, the laws and agencies involved, public education, and preliminary survey work. This portion of the book required very little revision. The subsequent chapters, concerned more directly with the practical application of control methods, has undergone extensive revision and enlargement. This has been necessary largely because of the information that has been obtained during the present war emergency. During the past four years, no doubt more people have been concerned with malaria and its control than during any previous decade. As a consequence a great deal of information has accumulated that is clarifying and expanding our knowledge of the subject. Some of this information has not been released for general consumption, but much of that no longer restricted has been incorporated into this book. For example, the application of D.D.T. as a larvicide is discussed. There are two notable additions to the appendix of the second edition. One is a large folding chart of the important malarial mosquitoes, showing their geographical distributions, typical breeding places, and the effective methods for their control. The second is a section on the identification of mosquitoes. It includes several simplified keys and eleven clear plates illustrating the various morphological structures of the mosquito.

M. M. BROOKE

GENERAL AND SYSTEMATIC ZOOLOGY

SEASHORE LIFE AND PATTERN.

By T. A. Stephenson. The King Penguin Books, Penguin Books, London and New York. 2s. 28 pp. + 16 plates. 1944.

The King Penguins are a growing series of small illustrated books, reminiscent of the prewar German series of the Insel-Bücherei. This particular volume is essentially a collection of decorative illustrations of seashore life. They are accompanied by a brief text in which the artist-biologist discusses how he creates artistic patterns by abstraction from and arrangement of the patterns found in nature. The colored reproductions attain a high standard, and are delightful.

ENTOMOLOGY FOR INTRODUCTORY COURSES.

By Robert Matheson. Comstock Publishing Company, Inc., Ithaca, N. Y. $5.50. xiv + 600 pp. 1944.

This well illustrated and attractive text is written in a fluent and admirable style. After a general introduction and a consideration of other classes of arthropods the author takes up the external and internal anatomy of insects, devoting an entire chapter to their mouthparts. A chapter on Development and Growth in Insects discusses metamorphosis, chiefly in a descriptive way. The main body of the book is devoted to a survey of 23 principal orders. There is an abundance of keys based on readily apparent structures. The North American species selected as examples have been chosen on the bases of abundance, economic importance, or interesting habits. The book concludes with four chapters on Insects in Relation to Human Welfare, a section that is full of interesting descriptions of insects as food or food producers, as scavengers, and as producers of various useful products; in relation to pollination; and in relation to human or plant diseases. A glossary, bibliography, and index are provided.

The book is a lengthy one, and few students will be able to master more in a single course. Yet, without a desire to cavil, it is disappointing to find here so little on insect physiology, particularly in regard to molting and metamorphosis, so bare a mention of protective coloration and mimicry, of modes of sex determination, or of the genetic and cytological studies that have made insects so important to science. Nor is there very much

on the social insects. Perhaps the most startling omission is the failure to consider the basis of behavior and the roles of instinct and intelligence in the varied life histories described.

These are faults of omission only, and with Imms, Wigglesworth, Cott, Wheeler, and others on the reference shelf, too much should not be made of them. The author set out to write an introductory textbook of entomology, and in this he has succeeded well.

BENTLEY GLASS

NEW AND LITTLE KNOWN PSELAPHIDAE (COLEOPTERA) FROM BRAZIL, COLOMBIA AND MEXICO, WITH KEYS TO MEXICAN GENERA AND SPECIES. *Bulletin of the Chicago Academy of Sciences, Volume 7, Number 4.*

By Orlando Park. Published by the Academy, Chicago. Paper. Pp. 227–267. 1944.

Six new species are described, and six are reported from new localities. The pselaphid fauna of the Pacific Slope of Mexico is discussed.

CHECKLIST OF THE COLEOPTEROUS INSECTS OF MEXICO, CENTRAL AMERICA, THE WEST INDIES, AND SOUTH AMERICA. *Part Two. United States National Museum Bulletin 185.*

Compiled by Richard E. Blackwelder. Smithsonian Institution, Washington. 30 cents (paper). Pp. 187–341. 1944.

GUIDE TO HIGHER AQUARIUM ANIMALS. *Bulletin Number 21.*

By Edward T. Boardman. Cranbrook Institute of Science, Bloomfield Hills, Mich. $2.00. 108 pp. 1944.

This attractive handbook on those native vertebrates of Michigan that can be reared in aquaria includes descriptions of one lamprey, twenty-nine fishes, six salamanders, six frogs, two toads, four tree-frogs, five snakes, and six turtles. Most of these forms are illustrated in excellent photographs, and each is briefly characterized as to appearance, size, habitat, breeding habits, and food. There is a short general introduction on aquarium-keeping. Brief appendixes on hardy exotic fishes, on water for the aquarium, and on the treatment of diseased fishes and diseased reptiles and amphibians conclude the book. There is a short bibliography of 22 titles, but no index. However, the table of contents will serve adequately in place of the latter. Teachers and aquarium fanciers should find the volume interesting and useful.

STINGFISH AND SEAFARER.

By H. Muir Evans. Faber and Faber Limited, London. 15s. 180 pp. 1943.

In pursuing the study of fish as a hobby, the British surgeon Muir Evans has concerned himself with diverse problems. This book is devoted especially to the poison spines and other offensive and defensive weapons of marine animals, to the knowledge of which the author has made a considerable contribution. He describes different types of fish, their habits, and the structure and histology of their poison spines and glands, and discusses the nature of the venom and its relationship to pigmentation. The result is a work of practical value, presented as a clear and popular discourse, as free as possible from technical jargon, and with many interesting digressions into related topics that indicate the author's extensive first-hand knowledge of his subject.

EILEEN SUTTON GERSH

A REVIEW OF THE HALFBEAKS OR HEMIRAMPHIDAE OF THE PHILIPPINES AND ADJACENT WATERS. *Stanford University Publications University Series. Biological Sciences, Volume IX, Number 2.*

By Albert W. C. T. Herre. Stanford University Press Stanford University, Calif. $1.00 (paper). 48 pp. 1944.

Twenty-four species of this family of fishes are described, along with one doubtful species, one variety, and one new variety. There are no illustrations.

THE PRAIRIE CHICKEN IN MISSOURI.

By Charles W. Schwartz. Conservation Commission State of Missouri, Jefferson City, Mo. $5.00. 91 pp. + 85 plates. 1944.

This collection of 85 remarkable photographs, including a kodachrome frontispiece, together with five black and white sketches and accompanying text, is an ornithologist's dream. Printed on heavy pebbled paper 9" x 12", bound in brown fabrikoid, and published at cost ($3.50), it has been limited to an edition of 2000 copies, a number which will inevitably fall far short of satisfying the demand. The use of the methods of the Limited Editions Club by the Conservation Commission of the State of Missouri in distributing this book of scientific value is to be deplored, especially its limited disposal to individuals at the pre-publication price, and the sale of the remaining 200 to book dealers for resale at collector's prices. It is to be hoped that the Commission will reconsider the matter and make a second printing for wider distribution.

THE WOLVES OF NORTH AMERICA. *Part I. Their History, Life Habits, Economic Status, and Control. Part II. Classification of Wolves.*

By Stanley P. Young (Part I) and Edward A. Goldman (Part II). The American Wildlife Institute, Washington. $6.00. xx + 636 pp. 1944.

Wolves belong to the carnivorous family Canidae, which is nearly world-wide in distribution and includes "man's best friend," the dog. Wolves have not only been a menace to human life, but have always been very destructive to domestic stock, being perhaps the most efficient of all predators. In ancient legends the wolf already figures as a symbol of sagacity, courage, and ruthlessness. Only in recent days and with the aid of modern traps and poisons has man succeeded in exterminating the wolves over a large part of their historic territories. From the point of view of human welfare, economics, history, and literature the wolves and their descendants, the dogs, represent the most important and interesting group of carnivores.

This large and scholarly volume deals with the two North American species of wolves, *Canis lupus* and *Canis niger*, but not with the closely allied coyotes. In the first two thirds of the book Young reviews the historical references to American wolves and discusses their past and present distribution, habits, economic status, and control. The second and smaller part, written by Goldman, is devoted to the taxonomy of the wolves in the New World.

Not long ago wolves still ranged over nearly all the vast land from the arctic zones to central Mexico, but to-day they have disappeared east of the Mississippi, excepting in northern Wisconsin and Michigan, and from most of eastern Canada and all of Newfoundland. Wolves begin to breed in their third year. The period of gestation lasts 60 to 63 days, and an average of seven whelps are born some time between April and June. A fully grown wolf, weighing about a hundred pounds, can gorge itself easily with eighteen pounds of meat at one meal. Wolves have very powerful jaws and effective dentition. One trapped animal severed with one snap a knotty juniper limb, two inches thick. In old wolves, i.e., after the age of about 12 years, the teeth become much worn and lose their cutting power, but the animal can still grab his prey by the throat and succeed in strangling it. The diet of wolves forms a long and varied list, ranging from berries, fishes, frogs, and birds to elk, moose, horse, and steer. It includes carrion, and even the wolf itself. Monetary losses to ranchers caused by wolves, after the buffalo had been replaced by cattle and sheep, reached huge sums. It led to the relentless pursuit of the killers by means of all sorts of devices, backed by high bounties, devices ranging from baited fishhooks, suspended from trees, to deadfalls, pits, wolf-scented traps, drives, and, most deadly of all, poisons. Wolf pelts repay only a small part of the cost of wolf control. Between 1738 and 1747 the Hudson's Bay Company alone sold over 10,000 wolf skins at prices varying between 9 and 18 shillings apiece, but in 1938, when few skins reached the markets, the price had risen to as high as 65 dollars for a prime pelt. That wolf and dog will cross readily and produce fertile offspring has been amply demonstrated.

In *Canis lupus* 23 subspecies can be distinguished; in *Canis niger*, 3. The two species and their numerous geographic variations differ quantitatively, rather than qualitatively, in regard to general size, color, detailed shape of the skull, and diameters of the molariform teeth. Individual variations in all these features are common and marked; in regard to coat color they can range from nearly white to almost pure black. It appears that the different local races intergrade extensively. This is shown for cranial characters by the long tabulations of measurements accompanying the taxonomic report.

The facts mentioned above are mere random samples of the great mass of detailed and comprehensive information, collected in this useful monograph on North American wolves. The book is generously illustrated by text figures and 131 plates. Of special value is the bibliography, filling 80 pages. Unfortunately there are no summaries, and the index is far too brief for such a large reference work.

ADOLPH H. SCHULTZ

LABORATORY MANUAL FOR INTRODUCTORY ZOOLOGY. *By C. Courson Zeliff. Published by the author, Harrisburg, Pa.* $1.50 (paper). 144 pp. 1944.

This manual is for a full year course. It includes studies of cells, tissues, mitosis, gametogenesis, and embryology, and a very extensive survey of the animal phyla. Directions are clear, concepts modern. There is no physiology, no genetics, no field work. A few illustrations are included.

ANIMAL EMBRYOLOGY

EXPERIMENTAL STUDIES ON ECTOHORMONAL CONTROL OF THE DEVELOPMENT OF SUPPLEMENTARY REPRODUCTIVES IN THE TERMITE GENUS ZOOTERMOPSIS (FORMERLY TERMOPSIS). *University of California Publications in Zoology, Volume 43, Number 17.*

By S. F. Light. University of California Press, Berkeley and Los Angeles. 50 cents (paper). Pp. 413–454. 1944.

Numerous experiments failed to supply conclusive evidence in support of the ectohormonal theory of reproductive inhibition, but the general trend of the evidence is favorable to it.

ANIMAL MORPHOLOGY

SPEED IN ANIMALS: *Their Specialization for Running and Leaping.*

By A. Brazier Howell.. University of Chicago Press, Chicago. $4.00. xii + 270 pp. 1944.

This book will be an anatomist's delight, for it is mostly anatomy, nearly naked and quite unashamed. The title however, is apt to be misleading. It should be "The Anatomical Basis of Speed in Vertebrates"—in fact, "in Mammals," for the reader will look here in vain for any information about the running and leaping of those groups of insects that are specialized for exactly that mode of locomotion, to say nothing of the controversial speeds of the deer botfly or the squid. Fish are treated briefly, omitting almost entirely the kind of work represented by J. Gray. Birds receive a disappointing two and one-half out of 262 pages. But to complain of this is to ask for another book. Once it is realized that this volume is frankly an account of those aspects of the subject that have been "of greatest interest to [the author] individually," the reader will gladly discover a great mass of anatomical facts about the bones and muscles concerned with locomotion, and something about various types of locomotion found in mammals.

After a description of the adaptations for speed and locomotion generally in the monotremes and the marsupials, the more important orders of placental mammals are discussed. This is followed by special chapters on the muscular system, the axial skeleton, the fore limb, the hind limb, proportions, and gaits. There is considerable emphasis, legitimately, we believe, on the horse. Altogether, an enormous number of facts have been gathered together around the concept of adaptation for getting from one place to another.

The author leaves for others a consideration of the physiological, neurological, endocrinological, and other aspects of speed in mammals. It is to be regretted that he did not treat the evolutionary explanation of these adaptations in the same way. The text is marred by recurring references to "the need for speed" and the varying ability of different evolutionary strains to "respond to it," or the "evolutional effort" that has gone into the anatomical specializations now existing. Such remarks, and others like them, are possibly intended as metaphors, a mere manner of speaking. Nevertheless, they will most certainly make anyone wince who knows something about the facts of genetics or the modern theories of evolution. A layman would surely be misled.

We were sometimes puzzled about the public for which the book is intended. On some pages even the most elementary words are most fully explained; on others a flood of technical terms is introduced with little or no prior explanation. What must happen to the reader who needs to be told the meaning of the origin and insertion of a muscle (both of which are fully explained) when he suddenly reads that the fibula is not supported by the calcaneus, that the astragalus has but a single pulley and rests solely on the navicular, and that the mesaxonial is such that the axis of the podial passes through the third digit? There should have been at least a glossary. Many topical comments suggest themselves. The account of camels and camel racing is noteworthy. The various gaits of horses are especially clearly described and illustrated with drawings made from frames of a slow motion picture. Perhaps, on the whole, the book has the faults of its virtues.

The illustrations are both pleasing and clear, though not very numerous, especially in view of the price of the book, which seems excessive.

G. B. MOMENT

TOPOGRAPHICAL ANATOMY OF THE DOG. *Fourth Edition.*

By O. Charnock Bradley. Revised by Tom Grahame. The Macmillan Company, New York. $7.50. xii + 316 pp. 1943.

Since the dog is one of the most widely used experimental animals, a first-class account of its anatomy is especially to be appreciated. That Charnock Bradley's well-known handbook, the English equivalent of Ellenberger and Baum's *Anatomie des Hundes*, now appears in its fourth edition is in itself ample testimony of its proven worth. In some respects it is a more useful work than its German counterpart.

The present edition represents a considerable revision, including a rewriting of certain parts and the introduction of some excellent x-ray photographs and new diagrams. The illustrations are uniformly of high caliber. The presentation remains topographical rather than systematic. Some subdivision of the text on the basis of regions, however, would have enhanced the utility of the book. There is one notable instance of regrettable terminology—perpetuation of that curious error of nomenclature, "nervi cerebrales" (in place of "nervi craniales"), perpetrated by the B.N.A.

W. L. STRAUS, JR.

BAILEY'S TEXT-BOOK OF HISTOLOGY. *Eleventh Edition. Revised by P. E. Smith and W. M. Copenhaver, with the assistance of Aura E. Severinghaus and Charles M. Goss. Williams & Wilkins Company, Baltimore.* $6.00. xx + 786 pp. 1944.

That this book, which first appeared just forty years ago, has gone through eleven editions, is a sufficient indication of its value. It has long been one of the most popular histological texts, especially in medical schools. No doubt its popularity deservedly will be continued.

The new edition has undergone considerable revision. Many new figures, both in color and half-tone, have

been included. The text has been brought up to date and extended by incorporation of recent work. A section on the placenta has been added. Selected references to the literature are appended to each chapter.

ANIMAL PHYSIOLOGY

THE LIVING BODY. *A Text in Human Physiology. Revised Edition.*

By Charles Herbert Best and Norman Burke Taylor. Henry Holt and Company, New York. $3.90. xxii + 571 pp. 1944.

In its revised edition, this book remains firmly among the leaders of its kind, and perhaps is without a peer. A shorter text of physiology, it is written primarily for use in college courses in human physiology, but also for courses given to nurses and dental and agricultural students. As such, it is necessarily condensed and dogmatic in contrast with the longer physiological texts. It is not, however, merely a condensed version of the larger, excellent treatise by the same authors, but has its own flavor. The simple, lucid, yet scholarly manner of presentation make it ideally adapted to its purpose.

Although the accounts of the functions of the various tissues and organs are preceded by descriptions of their structure, many of these are frequently all too brief or inadequate. At least this is true, in the experience of the reviewer, in respect to its use in courses in combined anatomy and physiology given to student nurses, who have need of something more than the most sketchy account of human anatomy. Because of this, it is difficult to use the book as a basic text, although it is excellent for collateral reading. This would apply to both the original and revised editions, for the latter has undergone no fundamental change in this particular feature.

The revised edition does contain, however, much new physiological material based on work that has been done since the book was first published in 1938, material relating to such subjects as hemoglobin, transfusions, clotting, hypertension, respiration, and vitamins. The 283 illustrations are uniformly well chosen and executed with great clarity.

W. L. STRAUS, JR.

MEDICAL ASPECTS OF AVIATION (SPEED AND ACCELERATION).

By Capt. Ernst Jokl. Sir Isaac Pitman and Sons, Ltd., London. 10s 6d. xiii + 104 pp. 1943.

The title is an overstatement of the scope of this little book. The author proposes to describe the medical problems of modern aviation, chiefly those created by speed and acceleration, to pilots, Air Force officials, medical practitioners and educated laymen. His simple, direct statements of the physical and physiological stresses encountered in modern aviation are for the most part clear and accurate. Numerous illustrations and accounts of experiences attract the reader's attention, and no one could fail to understand this discussion. One hopes, however, that the medical profession and Air Force personnel have advanced far beyond the need for such an elementary presentation of the physiological problems created by such factors as speed, acceleration, and exposure to high altitude. An educated layman will find little in this volume which he does not already know. Those who are actually dealing with aviation and aviation medicine can find other reviews and books that will be of much greater interest and aid.

PHYSIOLOGY IN AVIATION.

By Chalmers L. Gemmill. Charles C. Thomas, Publisher, Springfield, Illinois, and Baltimore. $2.00. vii + 129 pp. 1943.

This is a well-conceived small handbook designed to familiarize aviators with the changes in body function that tend to occur under conditions encountered in aviation. Such topics as the control of respiration, the carriage of oxygen by the blood, the effects of anoxia, aeroembolism, the effects of acceleration on man, temperature control, the physiology of muscular exercise, and others are clearly and briefly dealt with. Although the treatment of important problems is sketchy, this book would be very useful to physicians and excellent for the preliminary training of students, were it not for one defect. The carelessness of preparation has been such that both minor and major errors of grammar and fact occur throughout the book in such numbers that they cannot be ignored. The author has appended a list of thirty-seven corrections, but this list does not correct all the errors. No acknowledgments of the sources of the charts and tables used are given. Most of the graphs and many of the tables contain no statements as to units used, and even one who is familiar with the subject has difficulty in understanding them. If this book were corrected and reprinted, it would be useful to those interested in physiology and aviation.

SECRETORY MECHANISM OF THE DIGESTIVE GLANDS.

By B. P. Babkin. Paul C. Hoeber, Inc., New York and London. $12.75. xix + 900 pp. 1944.

The author has not attempted to review the whole of the literature concerned with the secretory function of all digestive glands. The material presented here has been derived chiefly from the work performed during recent years by the author and his associates. The

book deals mainly with the mechanisms regulating the secretory functions of the gastric, salivary, and pancreatic glands, while other digestive glands are dealt with to a lesser extent. The first five chapters are devoted to a discussion of the morphology of the secretory glands of this system. The next fifteen chapters describe the innervation, blood supply, secretory activities, and general function of the stomach. This group of chapters concerned with the gastric phases of the digestive process is followed by four chapters enumerating the hormones of the alimentary canal and their contribution to pancreatic, intestinal, and gastric function. The remaining chapters are devoted to a description of the regulation of salivary secretion, except the final two, which return to a discussion of the secretory process and the effects of nerves on the digestive glands. The reader is aided from time to time throughout the book by summaries of the conclusions that may justifiably be drawn from the data presented. In dealing with questions concerning which the available information does not permit a decision concerning the nature of the basic mechanism, the author presents the current hypotheses and the evidence pertaining to their validity. The analysis of the neural and chemical control of gastric secretion is detailed and clear, and, like the author's treatment of all the selected subjects, admirable. One of the most impressive features of this work is its completeness and comprehensiveness. No aspect of function, from the processes within individual cells to the functions of the organs and the intricacies of the controlling mechanisms, has escaped his attention. The bibliography is extensive and the index adequate. However, in seeking information concerning specific points, one must search the entire volume because various aspects of function are treated in several connections. Some individuals may not agree fully with certain of the author's interpretations, but it is inconceivable that any should feel other than admiration for this excellent treatise.

CHANDLER MCC. BROOKS

HEALTH AND DISEASE

MEDICAL EDUCATION IN THE UNITED STATES BEFORE THE CIVIL WAR.

By William Frederick Norwood, with a foreword by Henry E. Sigerist. University of Pennsylvania Press, Philadelphia; Oxford University Press, London. $6.00. xvi + 487 pp. 1944.

As this history ends long before the great reforms in the field of medical education, it contains, besides a description of brilliant beginnings in the 18th century, mainly the history of the "dark ages" of medical education in the United States. It is thus less a contribution to the history of medical progress, than to the history of civilization in this country. The author has collected with great industry the already existing but so far widely dispersed material on the numerous old American medical schools, many of them now extinct and to this he has added the fruits of his own extensive research. He has thus created a very valuable and reliable survey of a subject, which probably because of its being controversial up to a few decades ago, has attracted the attention of those interested in medical history almost more than the history of medicine proper, that is, the history of diseases and their treatment.

ERWIN H. ACKERKNECHT

X-RAY EXAMINATION OF THE STOMACH. *A Description of the Roentgenologic Anatomy, Physiology, and Pathology of the Esophagus, Stomach, and Duodenum.*

By Frederic E. Templeton. The University of Chicago Press, Chicago. $10.00. iv + 516 pp. 1944.

The aim of this book, as stated by the author, is to describe and deal in considerable detail with the newer x-ray techniques employed in examining the esophagus, stomach, and duodenal bulb, together with the clinical interpretation of the findings. This has been accomplished in a satisfactory manner. Descriptions of apparatus and examination procedures are given in the first four chapters. The fifth chapter describes in detail the normal anatomy and activities of the pharynx, esophagus, stomach, and duodenum. The remaining thirteen chapters are devoted to a very thorough discussion of the identification of the abnormalities produced by operations, neuromuscular disturbances, inflammations, peptic ulcers, neoplasms, and other pathological and nonpathological processes. Descriptions are extremely thorough and the illustrations are numerous and excellent. This book is highly recommended to those engaged in x-ray examination of the stomach. Anatomists, physiologists, and others who deal with the function of the gastro-intestinal system can also obtain much information from it, but these contributions are scattered and limited. For example, the physiologist will find that the motor activities of the esophagus and stomach which can be visualized by means of the x-ray technique are very thoroughly described and portrayed, but the discussions of their origin, control, and the causes of abnormalities are brief and not easily found. This book is a worthy contribution to the advance of roentgenology and should be a great aid to gastro-intestinal diagnosis.

CHANDLER MCC. BROOKS

HYPERTENSION AND HYPERTENSIVE DISEASE.

By William Goldring and Herbert Chasis. The Commonwealth Fund, New York. $3.50. xv + 253 pp. 1944.

This book is the product of fifteen years of collaboration between the Departments of Medicine and Physiology

of the College of Medicine of New York University. By design the work is a description of the authors' concepts of hypertensive disease, and the bulk of material presented is derived from their own clinical and experimental observations. As such, it is a clear and confident analysis of evidence concerning the cause, nature, and treatment of hypertensive disease. It is initially stated that the fundamental hemodynamic alternation in hypertension is an increased resistance to the outflow of blood in some greater or lesser portion of the systemic arterial bed. The essential criterion of the diagnosis of hypertension is abnormal elevation of the diastolic blood pressure. In hypertensive disease, due to the operation of those factors that normally control arterial pressure, it is illogical to conclude that variations in blood pressure are due to changes in primary disturbance or to use the level of blood pressure as an indication of the progress of the underlying disease. Rational therapy must be directed towards the still unknown mechanism which precedes vasoconstriction and the consequent elevation of pressure. The authors next discuss the clinical aspects of hypertensive disease and give a description of kidney, heart, retinal, and brain involvements. The concept of a prehypertensive phase is discarded as unsubstantiated. The following chapters, which are devoted to a description of the results obtained from well-performed measurements of cardiac output, arterial blood pressure, effective peripheral resistance, renal functional and hemodynamic alterations in hypertension, are admirably clear and convincing. The techniques used are described in the appendix. The chief theme of the book is stated in chapter six, in which the work on experimentally produced hypertension is briefly reviewed and compared with clinical observations. Here it is admitted that a primary renal mechanism has been established in the genesis of experimental renal hypertension, and that hypertension might be produced in man by the same technique. However, clinical evidence as analysed does not support the concept that renal ischemia is the primary etiological event in human hypertensive disease. The renal ischemia observed in hypertensive patients appears to be one of the sequelae of the hypertensive process. The authors' evaluation of medical and surgical treatment will disappoint many who have claimed high degrees of success from various procedures. The use of thiocyanate in hypertensive patients is held to be unjustifiable. Pyrogenic substances produce temporary lowerings of blood pressure, accompanied by various degrees of amelioration of symptoms, without, however, producing a correction of the fundamental disturbance. Treatment with renal extracts is held to be of benefit probably only because of pyrogenic reactions. Treatment with amine-oxidases have failed. Sympathectomies are in no sense a cure of hypertensive disease. Unilateral nephrectomy, omentopexy, nephropexy, and other surgical procedures are of no demonstrated value. These generalizations are abruptly reached, but the reasons upon which they are based are stated.

The conclusion one draws from this treatise is that the primary cause of hypertensive disease in man is still unknown. All the medical and surgical treatments thus far introduced are of no value in correcting the primary dysfunction, although they may evoke transient ameliorating effects by producing compensatory changes. The device proposed as the most valuable in rehabilitation of the hypertensive patient is psychotherapy. Though the general tone of the book may be displeasing to those whose hypotheses have been so briefly dismissed, it will be generally agreed that a concept of hypertensive disease has been well presented and skilfully supported, both by experimental evidence and by clinical observation.

CHANDLER MCC. BROOKE

YOUR EYES.

By Sidney A. Fox. Alfred A. Knopf, New York. $2.75. xiii + 191 + viii pp. 1944.

This is a fluently written and readable book for the layman, presenting in readily comprehensible form the answers which in the present state of knowledge can be given to the common questions that laymen ask about eyes and vision. The mechanism of vision, of light and dark adaptation, and of color vision is discussed. A simple outline of refraction is given, together with a discussion of why some people need glasses. The problems of illumination, of glare and sunglasses, and of the visual requirements of automobile driving are discussed. Simple and reasonable suggestions are included concerning the hygiene of the eyes and first aid for injuries. The most frequent diseases that require surgical treatment are discussed, and the layman is given an outline of what can reasonably be hoped for under competent care.

In addition, there is an excellent chapter on the most flourishing current quackeries regarding the treatment of eye defects. There is also a valuable chapter clarifying the distinction between optometrists and eye physicians. It is well that the layman should know that optometrists are not only untrained in the recognition of diseases of the eye, but are actually legally exempted from any responsibility in case a patient loses his sight as the result of their having incorrectly told him that his eyes were healthy. It would also be well for the layman to know that there are some physicians who practise as eye specialists without any special training in this field. State Medical Boards give identical examinations and identical licenses to those who become general practitioners and to those who become specialists, and there is no legal restraint preventing any licensed physician from calling himself a specialist. As the author wisely points out, the layman should ask his family physician for advice in selecting a specialist.

It is to be regretted that a chapter is not included on the cost of eyeglasses, a story involving price fixing and rebates in which neither optical manufacturers, optometrists, nor eye physicians are free from responsibility.

JONAS S. FRIEDENWALD

FERTILITY IN MEN. *A Clinical Study of the Causes, Diagnosis, and Treatment of Impaired Fertility in Men. By Robert Sherman Hotchkiss, with a Foreword by Nicholson J. Eastman. J. B. Lippincott Company, Philadelphia.* $3.50. xiii + 216 pp. 1944.

The National Committee on Maternal Health, as part of its program of promoting studies on human reproduction, has sponsored the publication of two volumes, of which this book is one, on the problems of sterility. Its author is a genito-urinary surgeon who has for twelve years conducted a pioneer clinic for male sterility. With the aid of the National Committee on Maternal Health he has had excellent research associates. He is evidently an enthusiastic student, an ingenious surgeon, and a humane practitioner. That part of the book which deals with clinical diagnosis and treatment represents careful thinking and thorough study of the individual patients. The delicate social and psychological problems which present themselves in this field of practice are sensibly and sympathetically treated. There is a full and interesting discussion of John McLeod's researches on the metabolism of spermatozoa, of the author's own studies of the variability of human semen, and of other recent work closely relevant to the practical problem.

Readers should be warned, however, that this book is not the place in which to study the general background of the problem of male infertility. As soon as the author gets away from his own immediate experience he becomes inaccurate and obscure. Part of this is due to poor writing. Merely inept English, which occurs on almost every page, may be forgiven to an author distracted by active military service, if not to the publisher and sponsors; but the language frequently confuses or obfuscates the reader, as on p. 33, where it is implied without reservation that sterile couples who adopt infants have children of their own shortly thereafter; or on p. 16, where it is said that "laboratories have found regular descendants of sterile males in colonies of mice." The account on p. 195 of the Rh factor, important as a possible cause of human sterility, is not intelligible. In other places it is clear that the author has tried to round out his discussion by introducing topics from basic sciences which he has not had time to assimilate, witness the passage on "heredity" (i.e. sterility due to genetic causes) which contains two gross misstatements, or the paragraph on the history of the male hormones, which fails to make clear the nature of Berthold's fundamental contribution and omits all mention of the fundamental chemical work of McGee and Koch.

In summary, this book contains valuable information for practitioners dealing with male infertility; properly pruned and edited it would be an excellent clinical textbook; but if the Committee on Maternal Health wishes, as it presumably does, to stimulate the interest of the medical profession in fundamental scientific problems in this field, so that clinical study may go forward on a sound basis, its purpose would have been better served, and the valuable experience of the author more fairly represented, had his contribution been given its proper place as part of a volume prepared by a group of specialists in the several aspects of the subject.

FERTILITY IN WOMEN. *Causes, Diagnosis and Treatment of Impaired Fertility. By Samuel L. Siegler. Foreword by Robert Latou Dickinson. J. B. Lippincott Company, Philadelphia.* $4.50. xv + 450 pp. 1944.

This is the companion volume to *Fertility in Men*, reviewed above, and like that volume represents the practical experience and the thought of an active specialist in the disorders of human reproduction. Practitioners in this difficult field will find in it a great deal of information on diagnosis and treatment. The program of study of the individual case is fully analysed. Technical procedures are carefully described. There is a good chapter on tubal insufflation ("Rubin test") and on hysterosalpingography (visualization of uterus and tubes by x-ray), the latter subject being illustrated with interesting roentgenographs. Treatment with ovarian and pituitary-type hormones is conservatively discussed.

Dr. Siegler quite properly views sterility in women as a biological problem and seriously tries to found his exposition upon the existing body of physiological knowledge. In this effort he has, however, wandered far from his own personal field of experience, to treat of biological and chemical matters at second- (and sometimes at third-) hand. The compilation resulting is not clearly focussed on the immediate problem, nor is it free from confusing minor errors and half-truths. The book cannot, therefore, be recommended without reservation to students of biology and medicine as a source of information on the general biology of human sterility.

THE AMERICAN ILLUSTRATED MEDICAL DICTIONARY. *A Complete Dictionary of the Terms Used in Medicine, Surgery, Dentistry, Pharmacy, Chemistry, Nursing, Veterinary Science, Biology, Medical Biography, Etc., with the Pronunciation, Derivation, and Definition. Twentieth Edition, Revised and Enlarged. By W. A. Newman Dorland, with the collaboration of E. C. L. Miller. W. B. Saunders Company, Phila-*

delphia and London. Plain, $7.00; thumb-indexed, $7.50. 1668 pp. 1944.

In this new edition the editors have followed their policy of presenting a revision of this standard reference work every three years. By eliminating some of the tables and portraits, they have made room for many new definitions without perceptibly enlarging the volume. New terms from biochemistry, chemotherapy, tropical and parasitic diseases, vitamin research, endocrinology, mycology, and especially from war medicine and surgery have been added.

General biological terms are defined so wholly from a medical standpoint that as general definitions many are unsatisfactory; a number represent antiquated conceptions—mitotic prophase, for example. It is also surprising that virtually no account has been taken of the developing knowledge of the hereditary aspects of many of the diseases listed. A few are said to be "hereditary" or "familial," but without any more specific definition of their mode of inheritance. So little effort has been made to modernize the dictionary in this respect that the criticism is true not only in instances where the mode of inheritance is doubtful, but even for such well established cases as the ordinary blood groups, the Rh factor, retinitis pigmentosa, and red-green color-blindness.

In spite of these shortcomings, this dictionary will be almost as useful on the desk of the biologist as on that of the medical student or practitioner.

BENTLEY GLASS

ANIMAL NUTRITION

AN INTRODUCTION TO FOODS AND NUTRITION.

By Henry C. Sherman and Caroline Sherman Lanford. The Macmillan Company, New York. $2.50. viii + 292 pp. 1943.

This book is a timely one. It has been written, as the authors say in their preface, "to aid the solution of the practical problems of adjustments to the food supply and rationing conditions of today and tomorrow and to develop the educational value of resourceful use of nutritional knowledge in a changeable situation as to availability of individual articles of food."

To achieve the purpose stated above, the authors have divided their book into four main parts, namely:

I. Individual and National Importance of Nutrition.
II. The Maintenance of Good Family Nutrition; Difference in Need due to Age, Sex, and Occupation.
III. Foods; Their Properties, Preservation and Preparation.
IV. Planning of Meals and Management of Food Supplies.

In the first part there has been included a brief discussion of the standards of good nutrition, the food needs of the individual, and the proper food selection to maintain good nutrition. A discussion of the national nutrition problem, including quotations from the first National Nutrition Conference, held in Washington, D. C. in May, 1941, is included.

The second part of the book includes a very brief discussion of the essentials of an adequate diet: calorie value, proteins, vitamins, and a few of the minerals. This part of the book contains the essential information written in a simple way for a non-scientific person. Detail of any kind is lacking.

The third division of the book contains much excellent information about foods. There are chapters devoted to "Milk and Its Products," "Meats, Fish, Poultry, Eggs and Nuts," "Fruits and Vegetables," "Breadstuffs and Cereals," "Fats and Sweets," "Food Adjuncts," and "Preparation of Food to Retain Nutritive Values." These pages are filled with instructive data about these foods, both as to the production of them, and their nutritional value.

The last division of the book includes a discussion of meal planning and gives a few sample menus.

The last chapters of the book deal with budgeting and purchase of foods. The authors limit themselves to a discussion of this chiefly "from the viewpoint of so investing the money available for food as to secure the best results in nutritional well-being." Some information is included about the grading and standardization of fruits and vegetables.

The book is concluded with a discussion of the individual and public nutrition policy: "Undoubtedly any sound nutrition policy, whether individual or national, and whether for the immediate situation or for a permanent future, should take due account of the findings of recent scientific research."

This book is written in an interesting, clear style, is concise, and contains much useful information. At the end of each chapter, there are exercises for the reader to use to test his understanding of the information given in the chapter. There are also listed "Suggested Readings," with very helpful comments by the authors on the listed articles.

In their preface the authors state that "This volume seeks to serve anyone interested in foods and nutrition, whether or not with a background of previous study of science." Because this purpose is so well achieved, the book would not be an adequate text for a scientific nutrition class, but it could easily be used in non-scientific groups.

MARGUERITE M. SCHMIDT

NEW ASPECTS OF CHEAP FOOD: *with a Table of Foods in alphabetic order showing in a single figure the comparative value in nutritive units of potato.*

By Rudolph Keller. Research Books, Ltd., in association with Wm. Heinemann, London. 1s 6d (paper). 52 pp. 1943.

This pamphlet is a paper-bound war edition of 50 pages, written by a professor from the University of Prague now living in England. There is apparently no plan of organization in this pamphlet. It consists of a group of twelve articles, in which the author airs his views and grievances. Apparently he is attempting to improve the English dietary in their rationed country, for he gives some general rules which the British should follow. These are good enough rules, but are not as complete and adequate as those which we in America advocate.

The author also attempts to give in one figure an estimate of the nutritional value of food. "This estimate is based on a comparisop with potatoes, today the staple food of the poorer part of the community and thought to be the cheapest food, which it is not actually."

The pamphlet is poorly written, and the information not well expressed. In fact, it is so poorly expressed that on first casual reading one thinks that many of the statements are in error, until one perceives their real meaning. There is little of value in this pamphlet, particularly for those outside of England.

MARGUERITE M. SCHMIDT

GENERAL PHYSIOLOGY

MEDICAL PHYSICS.

Edited by Otto Glasser. The Year Book Publishers Inc., $18.00. xlvi + 1744 pp. 1944.

This book is an ambitious attempt to supply, in the form of an encyclopedia, a text and a working manual for the application of physics to medicine. An extensive amount of information has been collected by Dr. Otto Glasser, Editor-in-Chief, and his twenty-three co-editors on many physical and physical-chemical phenomena of importance in medicine; much of this information would be difficult to locate unless very extensive library facilities were available. The field of application of physics to medicine is so wide that it is hardly possible to cover it in one volume. It is for this reason rather surprising that 53 pages are devoted to "bioelectricity," many phases of which are also discussed under different headings. In contrast to this, only 6.5 pages are spent on colloid chemistry and nine pages are given to "cosmic rays," a subject which at present is of very limited interest to medicine. The use of radioactive tracers in biological work—a subject of great immediate importance to medical research—is discussed in two pages.

The usefulness of this volume as an encyclopedia is reduced considerably by the peculiar arrangement of literature citations, which are 1) arranged in alphabetical order by the names of the senior authors; 2) each preceded by a number following the consecutive order of the first use of the references in the text. Since the name of the author of the reference is often not used in the text, but the number only, it makes it difficult to locate a reference in the bibliography.

Some chapters carry practically no references; for instance, the chapter on disinfection (one reference) and the chapter on the electron microscope. This latter chapter discusses the product of one manufacturer only. Very little reference is made to previous models, some of which have proved quite successful in electron microscopy.

The omission of many topics which could be useful in such a volume can probably be explained by the fact that investigators, who in 1940 were quite ready to contribute a chapter to this volume, found themselves in 1943 involved in war work that made it difficult to fulfil their promise.

The editor and publishers are to be congratulated for their courage in bringing out such an extensive volume under war conditions. It is very much to be hoped that a more balanced distribution of topics can be accomplished in successive editions.

The volume, with its wealth of information, has already proven to be of great help in the reviewer's laboratory. It can be highly recommended to anyone who is interested in the application of physics to medicine.

BIOCHEMISTRY

ANNUAL REVIEW OF BIOCHEMISTRY. *Volume XIII. Edited by James Murray Luck and James H. C. Smith. Annual Reviews, Inc., Stanford University P. O., California.* $5.00. ix + 795 pp. 1944.

This volume contains much that will be of interest to biologists. It is evident from these contributions that the productivity in this field has not been diminished. In reviewing such a group effort, it is impossible to make general statements that will apply to all chapters. It is, however, possible to place review articles in one of two groups. The first group contains reviews that may be called annotated bibliographies. The second group contains reviews in which a large amount of factual material has been arranged and presented in a clear, critical, and discerning manner that is possible only when the author has a profound knowledge of the field. This year's review contains many contributions in the latter class. Some of those that are of greatest interest to biologists will be mentioned in this review.

"Biological Oxidations and Reductions," by D. E. Green and P. K. Stumpf, brings up-to-date Green's excellent book on this subject. The discussion of "Non-Oxidative Enzymes" by Mann and Lutwak-Mann is a discussion of enzymes of another type and includes much material on phosphatases and choline esterase. The review of the work bearing on the structure of the intact protein molecule, by Neurath and Greenstein, belongs to the group of discerning reviews.

The review by Koch of recent chemical work on bile acids, sterols, steroid hormones, and their metabolism is also excellent, in spite of the fact that some of the best papers on this subject have not been included. The article on "The Biochemistry of Malignant Tissue," by D. Burk and R. J. Winzler, can be recommended not only for its organization, but also for the vast amount of information which it summarizes. They have selected 621 papers from the more than 2000 recent original papers in this field for discussion in the space of 26 pages. Of special interest to biologists is the contribution of D. Glick on "Histochemistry." This deals with the histochemical identification and determination of some of the vitamins, enzymes, and hormones. It also includes some work on micromethods such as Cartesian diver micromanometric metabolism studies, electron microscopy, and high-speed centrifugation.

FRANK H. J. FIGGE

ADVANCES IN ENZYMOLOGY *and Related Subjects of Biochemistry. Volume IV.*

Edited by F. F. Nord and C. H. Werkman. Interscience Publishers, New York. $5.50. viii + 332 pp. 1944.

The interrelationships of chemistry and biology are apparent in this volume. However, one wonders in reading it whether the cooperation and interchange of ideas in these fields is as close as it should be. *Advances in Enzymology* consists essentially of the views of a group of biochemists on the problems of biology and medicine. There is apparently no attempt to restrict speculation or to standardize the papers. There is thus considerable variation in the contributions and each must be evaluated separately.

An example of a speculative contribution is that of Gulick on "The Chemical Formulation of Gene Structure and Gene Action." It is clear that in the field of genetics, the biologist has forged far ahead of the chemist. This article is an attempt on the part of a chemist to bridge the gap. One must agree with the comment at the end of the article "that the direct and explicit aid rendered by chemistry to the understanding of genetics and biological evolution has been rather limited, though with the promise of more to come; but that aid by way of supplying patterns of thought and pertinent analogies has already become very important." It is a thought-provoking article.

The contributions of Pigman on glycosidases and of Herbst on "The Transamination Reaction" are critical and thorough. The chemistry of tyrosinase has been ably and clearly discussed by Nelson and Dawson. It apparent from the clear, convincing discussion that the authors have worked in this field for many years and have a thorough knowledge of the chemistry of this enzyme. It is, therefore, appropriate for the review to be limited to the chemistry of the enzyme or the *in vitro* experiments of the authors and a few other workers. Even a speculative attempt to correlate these purely chemical data with some of the *in vivo* work on pigment formation would have made this a more valuable and comprehensive review for biologists. It is regrettable that biologists and chemists, in this field of natural pigments, have a tendency to travel in separate spheres.

The review of Hotchkiss on "Gramicidin, Tyrocidine, and Tyrothricin," the substances derived from bacteria that have antibacterial activity, is timely. It includes much that is fundamental in the field of bacterial physiology; some of this may find application in studies on the mechanism of action of other chemotherapeutic agents.

The discussion of "Biological Energy Transformations and the Cancer Problem" is an attempt to link the etiology of cancer to the conversion of a nonspecific enzyme x into a "cancer virus." Just as other theories on the etiology of cancer, this is somewhat speculative. It contains much information on the enzymology of normal and malignant cells.

The chapter on "The Influence of Hormones on Enzymatic Reactions" is conspicuous for its brevity. The meagre amount of existing knowledge which has been included indicates that investigation in this important field has been neglected. The search of the literature has not been too exhaustive, however, as the influence of sex hormones on serum acid phosphatase and on tyrosinase were not mentioned.

The section on "The Absorption Spectra of Vitamins, Hormones, and Enzymes" is a concise and informative discussion. One very valuable feature is the inclusion of many graphs of characteristic absorption spectra of vitamins, hormones, and enzymes.

FRANK H. J. FIGGE

THE CHEMISTRY AND TECHNOLOGY OF FOOD AND FOOD PRODUCTS. *Volume I.*

Edited by Morris B. Jacobs. Interscience Publishers, Inc., New York. Both volumes, $19.00; singly, $10.50. xv + 952 pp. 1944.

This is the first volume of an exhaustive treatment of the chemistry and technology of food. The forty-one contributors to the two volumes have made an ambitious and successful attempt to prepare a unified, authoritative account of the various phases of the subject from the point of view of specialists in these fields. The list of contributors, therefore, includes food technologists, chemists, physicists, biochemists, bacteriologists, pharmacologists, sanitary engineers, food inspectors, and entomologists. The twenty-three chapters in the first volume were written by twenty-one collaborators.

The first eleven chapters, on fundamentals, deal with the aspects of food chemistry that are common to all foods. Physical chemistry, carbohydrates, lipids, amino acids, proteins, enzymes, vitamins, hormones, minerals, digestion, and fate of food-stuffs comprise the main chapter headings in this section. It is a complete, yet concise coverage of the chemical aspects of food. If this part of the book were to be published separately, it could, with minor additions, serve as a textbook of physiological chemistry for colleges. The physiological coverage, which is of secondary interest, is not as complete as the chemical.

Some of the chapters on the section on fundamentals of food chemistry are applicable to other biological specialties and are so well written that they deserve special comment. The chapter on the chemistry of amino acids and proteins is a remarkably well organized and clear presentation of the elementary facts and also includes the recent work in the field. The references to other reviews and to original work are numerous. The same may be said of the chapter on enzymes by Stern. This very clear, concise, and up-to-date account can be recommended to the biologist who wishes to either review or become acquainted with the fundamentals of enzyme chemistry. The discussion of vitamins in the chapter on vitamins, vitagens, and hormones, appears to be an abstract of the author's very excellent book on this subject. For many, this discerning condensation will perhaps be advantageous.

A more complete discussion, or perhaps a special chapter, on the symptoms resulting from deficiency of various food substances could have been included in a comprehensive work of this kind. Perhaps this will appear in the second volume. The supplementation of foods and food products with vitamins and minerals could also have been placed in this part on general fundamental food chemistry, perhaps as a special chapter. Omissions as well as duplications, while unavoidable in such a collaborative effort, are rare. However, the addition of iodine to salt as a goiter preventive is not mentioned in the discussion of either iodine or salt as food factors. The enrichment of flour is fully discussed in the chapter on cereal grains; and the fortification of milk and milk products is briefly mentioned.

In the second part, an organized account of all the basic types of foods is presented. In most of the chapters in this section, an account of the history, definitions, standards, composition, and chemistry of the various basic foods are given. The data were collected from widely scattered sources in the scientific and technical literature, and numerical values have been condensed in the 179 tables included in this section. The subject index of 50 pages appears to be adequate and facilitates the use of this volume as a reference book, for which purpose it was intended.

FRANK H. J. FIGGE

SOYBEAN CHEMISTRY AND TECHNOLOGY.

By Klare S. Markley and Warren H. Goss. Chemical Publishing Company, Inc., Brooklyn. $3.50. vii + 261 pp. 1944.

This is a timely book on the chemical and technical aspects of the versatile soybean whose industrial and food uses are rapidly expanding. It is a summary of the numerous research contributions and references that have appeared in the literature up until 1943. One of the authors is a soybean chemist and the other is a chemical engineer; both have been active in the research field covered by the book, which appears to be authoritative, thorough, and complete. The book will be welcomed by those working in the field, for it is a well organized and clear presentation of a large amount of factual information. Biologists and biochemists working in the fields of edible oils and the vitamin and protein supplementation of foods will find the book useful.

Part I, which deals with the chemistry and physical properties of soybeans and soybean oils, covers phosphatides, antioxidants, and vitamins at greatest length. Proteins, enzymes, carbohydrates, glycosides, pigments, and sterols are also discussed. Part II reviews the historical development of soybean processing. It also describes in detail the most up-to-date methods and machinery for processing, extracting, and refining soybean products. Finally, there is a discussion of the processing of soybean oil for food uses. The more recent developments in the use of soybean products in plastics and possible industrial uses were not included.

FRANK H. J. FIGGE

THE CONSTITUENTS OF WHEAT AND WHEAT PRODUCTS. *American Chemical Society Monograph Series Number 96.*

By C. H. Bailey. Reinhold Publishing Corporation, New York. $6.50. 332 pp. 1944.

This monograph is a compilation of the existent literature dealing with wheat and the substances that it contains. The first chapter relates the early researches on wheat proteins and includes a table showing the flour protein nomenclature arranged chronologically from 1728 to 1904. Chapters on prolamines, glutelins, water and salt soluble protein, crude protein, and crude glutein follow. These chapters contain summarized accounts of the various methods of hydrolysis and extraction of these substances, methods for the determination of the proteins, methods for the determination of the molecular weights of the protein, and methods for the determination of the products of hydrolysis of the wheat protein. There is also included in the chapter on crude protein and crude glutein a discussion of the variation of protein content in wheat grown over a wide range of territory that exhibits a

great range of soil types and climatic conditions. Tables and distribution curves help to clarify this information.

The other chapters discuss nucleic acid, non-protein nitrogen, starch, sugars, other carbohydrates, lipids, minerals, halogens, sulfur and selenium, acidity, pigments and vitamins of wheat and wheat products. These chapters also contain summaries of the original literature. They are concise and tables are quoted that help also to summarize the information. The author of the monograph comments on the various reports and points out conflicting ideas in the literature. The chapters are well organized, each beginning with a brief historical introduction. At the bottom of each page one finds the references to the original literature cited on that page.

This monograph is of great value to anyone interested in wheat and its constituents. It gives excellent, concise information for the technical worker and abundant references for those who want more detailed information.

MARGUERITE M. SCHMIDT

WOOD CHEMISTRY.

Edited by Louis E. Wise. Reinhold Publishing Corporation, New York. $11.50. x + 900 pp. 1944.

This book is a successor to *The Chemistry of Wood* (1926), by L. F. Hawley and L. E. Wise, Monograph No. 28 in the American Chemical Society Series of Scientific and Technologic Monographs. It represents an expansion in scope as well as a modernized treatment of the subject matter. It is a compendium written by thirteen authors, each contributing one or several chapters on his own field of specialization. It is divided into six parts, as follows:

I. The Growth, Anatomy and Physical Properties of Wood.
II. Components and Chemistry of the Cell Wall.
III. The Extraneous Substances.
IV. Surface Properties of Cellulosic Materials.
V. The Chemical Analysis of Wood.
VI. Wood as an Industrial Raw Material.

Emphasis is placed on recent research on various phases of wood chemistry and related fields. The treatment is not general but is one of selected topics which are thoroughly covered, with respect to basic information and principles, technique, and evaluation of needs and trends of future work. Of particular interest to the biologist, as well as to the workers in the numerous specialized branches of wood technology, are several chapters on borderline fields, such as an extensive treatment of the structure of plant cells that includes aspects of growth and morphology; a discussion of "plant cellulose" vs. true cellulose; the chapters on surface properties and colloidal behavior; and the last, timely chapters on the decomposition of wood by microorganisms.

FOLKE SKOOG

PSYCHOLOGY AND ANIMAL BEHAVIOR

PSYCHOLOGY IN LIVING.

By Wendell White. The Macmillan Company, New York. $2.50. x + 333 pp. 1944.

This book, by the author of *Psychology of Dealing with People* and of *Psychology of Making Life Interesting*, contains the substance of these two earlier books. It was prepared with the assistance of evening-school students of the University of Minnesota, to whom preliminary drafts were given in mimeographed form. It has, therefore, grown out of a very practical situation, one which demands that materials be presented in nontechnical everyday language.

We believe that the book must have met the specific needs admirably. It is stimulating, challenging, and interesting. And, though sufficiently full, it is concise, not being weighted down with wordy details of case studies which the formal textbook in mental hygiene usually has.

The book has two main divisions: Part I, "Psychology in Personal Relationships" (108 pp.), and Part II, "Psychology in the Achievement of Mental Health" (208 pp.). The chapter titles in Part I can be only barely suggestive of the materials and of the skill with which the author presents the different facets of behavior that may be grouped under the term "tact." This is one of the best presentations we have seen. Instead of presenting the usual case studies, the author weaves really practical materials, with a few sentences, into his context. The methods are often presented in a series of tactful, aphoristic statements. The chapters are: "Indirect Presentation of Ideas", "Direct Presentation of Ideas", "Inoffensive Opposition to Ideas", and "Misuse of Psychology." It is these chapters, especially, together with other chapters mentioned later, which distinguish this book from discussions only partially overlapping Dr. White's and from the more formal presentations in textbooks on mental hygiene, mental adjustments, or abnormal psychology.

Besides the chapters which deal with such usual topics in abnormal psychology as "Problems of Mental Health", "Unwholesome Adjustments", "Daydreaming", "Rationalization", "Extrusion of Thoughts from Consciousness," "Wished Physical Disabilities", and "Prevention of Unwholesome Adjustment", several of the remaining chapters are especially attractive as to content, treatment, and practical value. These are the chapters on "Pride-Sustaining Activity", "Freedom," and "Love." Besides these vital motives in human life, there are other strong ones, such as are indicated by the headings "Respectable Living and

Working Conditions", "Interesting Experiences", "Interesting Occupational Experiences", "Interesting Recreational Experiences", "Social Contacts", and "A Livelihood and Sense of Security." In the latter half of the book, Dr. White draws upon a number of relevant objective studies.

A set of "Self-testing Exercises" at the end, consisting of 133 statements quoted from the book, is presented by the author for the reader to use in trying to recall what was indicated in the text as well as elsewhere.

The author emphasizes the "constant need of our being versed in the science, and skilled in the art, of dealing with people. Competence in the directing or influencing other persons, and in managing one's own life, includes essentially an understanding of human nature." Strong though the "sense of personal worth" may be, the author points out that no one of the fundamental motives can be called "a master passion, since each in turn may swallow the others." "Other motives may (and do) in alternation take precedence over this one."

This book is one to be recommended to the general reader for his own self-improvement, as well as to teachers of classes on practical psychology and mental hygiene. The author's invigorating spirit is bound to be transmitted to others, and especially to those who need most to understand their own motives and maladjustments, and to learn how to make such adjustments most sensibly to the needs and requirements of their household and society.

C. HART WESTBROOK

PRACTICAL PSYCHOLOGY.

By F. K. Berrien. The Macmillan Company, New York. $4.00. xii + 584 pp. 1944.

"The author's aim throughout this text," he writes, "has been to survey the chief problems in which the applied psychologist has made some contribution"; "to present sufficient background information for the reader to understand, first, the significance of the problem, and second, the broad principles upon which the psychologist's contribution is based." The experimental studies summarized in the text (and there are enough of them to give a good picture, without so many as to weary or annoy the average serious reader) were selected "largely because of the degree to which they represented 'field' as contrasted with 'laboratory research,' even though a field study may only verify a conclusion previously established more accurately in a laboratory." The author believes that many previous texts in this field have "lacked a realistic tone because of their emphasis upon pedantic-appearing laboratory investigations, and, secondly, the student and the layman are more readily convinced of many propositions by reference to studies made outside the highly controlled conditions of academic laboratories." He also thinks the layman and the student (perhaps, better, the *beginning* psychology student) are "more interested first in conclusions and, second, in the evidence and procedures upon which these conclusions are developed." For these reasons the book has been written primarily for those with little or no previous contact with the usual elementary psychology course. Except for the chapters on "Study Efficiency," "Psychology and Learning," and perhaps those on "Principles of Mental Hygiene," "Mental Hygiene and Guidance," and "Vocational Guidance," this book has no more material in common with a present-day elementary psychology course than the occasional illustrations which the author of the general psychology might draw from findings in the various fields of applied psychology. For this reason and the aims stated by the author himself above, the text should prove to be an excellent introduction to "practical psychology" and should entice a thoughtful reader and student to follow up this introduction with a thorough course in general psychology, and, later, perhaps, more advanced work.

The chapter on "Adjustments in Old Age" adds much to the value of the book, for it comprises material which is only beginning to be treated in separate chapters in psychology books (except in books on developmental psychology) and to be given the prominence it requires, especially with the increasing proportion of older persons in our population. This chapter is very well done and will be both interesting, practical, and suggestive to those who themselves are in the period of "later maturity" (just before 60) as well as to those who have passed 60 and are classed by the author as "senescent." Then, too, there is much which should warn and guide the young person in his own preparation for old age, as well as give him a better understanding of, and consideration for, the older persons around him.

The style is smooth, readable, and interesting. Avoidance of technical terms, a generous provision of clear, attractive graphs and pictures, freedom from too many, too long, or unattractive tables, a good size of type and the excellent choice and organization of the material, all help to make the book one of the best we have seen for its purposes. It could well be used with adult education classes or evening classes for those who wish to follow up interesting leads and get practical everyday help rather than to earn 'credits' or work for degrees.

C. HART WESTBROOK

LIVING WITH CHILDREN.

By Gertrude E. Chittenden. The Macmillan Company, New York. $1.75. ix + 163 pp. 1944.

This comprehensive and graphic little volume might well be called a handbook or manual. It should appeal both to students and to parents. It deals with boys

and girls from birth on through the college years. The characteristics of various phases of growth and development and some reasons for behavior are considered. No one age group or phase is emphasized to the exclusion of another. For instance, the first chapter includes children of preschool, grade, and college age. Physical and physiological, mental, emotional, and social phases are given equal weight. Examples are described of a four-year-old boy, a grade school girl, a college freshman girl, a college boy-president of a dormitory,—all forming social patterns under their respective surroundings. The content of the book is thought-provoking, and in no place does the author dictate or impose her opinions. The text, with its excerpts from studies and books and its many graphic descriptions of children of different ages in a variety of everyday situations, helps the reader to form his own answers. Chittenden makes use of the works of well known and recognized authors and specialists in the fields of anthropology, psychology, child development, psychiatry, and sociology. A student of community hygiene and sociology should profit by this book, as should a student of child development. Parents will note that old theories and beliefs are not ignored but are questioned rationally, and more recent attitudes concerning the child's learning to walk, talk, sleep, and eat drive away old bugaboos and worries.

The author does not take a "holier than thou" attitude about our culture, as so many people are prone to do. Instead, she invites us to weigh our social patterns and compare them with those of the Samoan people studied by Margaret Mead. The reader will be reminded of the significance of the quotation—"All men are created equal"—when he reads, "There is a belief in our culture that any child, regardless of his capacities and limitations and of the difficulties he faces, can reach any goal that is set up for him. Needless to say, this belief is a fallacy, but the fact that it does exist probably accounts to a large extent for the American's great urge to be successful." The meaning of democracy flows through the text. It is not preached; principles are not theorized; instead sound facts are looked squarely in the face. No reader can fail to see the importance of the "family as a laboratory for democracy" or to be impressed with the responsibility of the home and community to the child.

The book deals with current problems arising from wartime conditions and the present-day interests of children in comics and radio. Nearly seven-eighths of the footnote references are dated between 1933 and 1943. The last chapter classifies books and pamphlets under such headings as prenatal care, children's clothing, and sex education. These latter forty-one references are well annotated and include the literature from 1932 to 1943. An average of four to five well selected references, ranging from 1937 to 1943, follow each of the first seven chapters. Many of the book's references, including those in the footnotes, are those undergraduates in courses in child development use. Subheadings are introduced by a paragraph that orients the reader for the discussion to follow, and a simple, concise summary comes at the end of each chapter.

CLAIRE QUINCER

THE BRUSH FOUNDATION STUDY OF CHILD GROWTH AND DEVELOPMENT. I. PSYCHOMETRIC TESTS. *Monographs of the Society for Research in Child Development Volume VIII, Number 2 (Serial Number 35).*

By Elizabeth Ebert and Katherine Simmons. Society for Research in Child Development, National Research Council, Washington. $1.50 (paper). xiv + 113 pp. 1943.

This monograph represents the psychometric fruits of the eleven-year Brush Foundation study of the growth and development of a large number of Cleveland children. The main results are based upon longitudinal studies of a sampling of superior children. The work has been painstaking, with hardly a detail unturned that might yield a possible relationship. The results include comparisons between the 1916 and 1917 Stanford-Binet scales, between these scales and several performance tests, data on sex differences, on the validity of the Otis group tests, on various test-retest coefficients; they furnish further data on losses and gains in I.Q., add to the accumulating evidence concerning the relative effectiveness of preschool tests in the prediction of later standing, and to the evidence concerning the apparently genuine changes among some children in the rate or tempo of mental growth. In the light of the recent interest in using terminal status as one of the criteria for the selection of test items, the data are interesting that show correlations between previous test scores (Binet and performance) and standing on Progressive Achievement batteries in the junior and senior high school grades.

The work of these investigators in straightforward reporting of statistical relationships is valuable in this period of a renewed critique of mental tests. It is unfortunate, however, that they failed to use the concentrated insight that this large study must have given them, either to put their own results into a clearer perspective or to project with vision the problems for the future raised by their own work and that of others!

THETA WOLF

PERSISTENCE AND CHANGE IN PERSONALITY PATTERNS. *Monographs of the Society for Research in Child Development, Volume 8, No. 3 (Serial No. 36).*

By Katherine Elliott Roberts and Virginia Van Dyne Fleming. Society for Research in Child Development, National Research Council, Washington, D. C. $1.50 (paper). vii + 206 pp. 1943.

This monograph is an attempt to study the personality development of college women in three of their life stages ("pre-college," "college," "post-college") in order to determine qualitatively and quantitatively the persistence and fluctuation of their personality patterns. It is based upon twenty-five extensive case studies from the files of the Merrill-Palmer Advisory Service for College Women, and utilizes excerpts from these voluminous life-histories as primary material for analysis.

The authors proclaim their belief in a dynamic, integrative concept of personality, but their procedure results in an atomistic description that precludes any such personality. They have created 523 attitudes and 229 traits (sic!) by which they pretend to classify personality, and then proceed arbitrarily to impose this "system" upon their material. The evidence is discovered from a case history in which the subject herself was the witness for it, and evidence applicable to the present study was not asked for according to any organized plan. One finds it difficult, too, to accept the authors' distinction between their "traits" and "attitudes." For example: if a person "lets children solve their own problems," she exhibits an attitude; if the same person "tries to solve problems rather than avoid them," she exhibits a trait. Moreover, in making distinctions *within* the traits, the authors place in *separate* categories such subjective terms as "excitable," "explosive," "impulsive." A kind of behavior, then, might be labelled "explosive" at one "life stage" and very conceivably be called "impulsive" at another stage, with results indicating fluctuation in pattern; a different labelling would, on the other hand, have shown persistence. Furthermore, if this kind of behavior did not happen to appear again *in the case history*—at another life stage—the results were treated as though the behavior did not occur, although it is clear that it simply may not have been reported. This fact irreparably and unaccountably affects the results.

Again, in the case histories, a false picture of persistence or of fluctuation is given because the setting of the behavior—or its meaning to the individual—had to be ignored. A person who may always be "sensitive" in a given social situation might conceivably "persist" in this behavior throughout the three stages, but in accordance with the plan in this study, because she was sensitive in situations x and y, and *not* sensitive in situations a and c, the "trait" is tabulated as fluctuating.

These conscientious authors very evidently wished to draw some important educational lessons from this study. It is regrettable that so much honest work was spent upon such an unproductive project. The material might have been studied from the point of view of integrated personality. A fair sampling of the case histories, analysed and briefed in a non-statistical manner, could have given evidence both of the persistence and modifiability of human behavior that was colorful, dramatic, and useful. On the other hand, it is abortive to attempt to force into statistical units material collected without method, without defined aim or uniformity, and replete with gaps that, if filled, might have changed the results altogether.

THETA WOLF

THE MEASUREMENT OF ADULT INTELLIGENCE. *Third Edition.*

By David Wechsler. The Williams & Wilkins Company, Baltimore. $3.50. vii + 258 pp. 1944.

In this third edition, the author's aim has been "to increase the book's usefulness to those engaged in the field of applied psychometrics." He has in mind particularly the military applications of the Wechsler-Bellevue Scale, now being used by some of the armed services of Great Britain as well as by those of the United States. The numbers and titles of the chapters have not been changed from those of the second edition; but chapters 6 and 11 have been "somewhat extended and in part rewritten," and contain most of the changes that have been made.

One outstanding value of the Bellevue Scale is that it enables clinicians to measure and score separately by the Verbal and the Performance Scales the two distinct groups of abilities or capacities, verbal and performance, which in some other widely used tests are measured by a single scale and indicated by a composite score. This composite score has concealed certain significant deficiencies and has thereby tended to mislead those who have accepted and dealt only with the final result, the figures for M.A.'s and I.Q.'s.

Another value of the book is that the extension of the Scale to mental levels higher than those measured by any other but Thorndike's CAVD Scales makes possible the mental measurement of persons up to the age of 60 years, and by a process of extrapolation, "without serious error by the use of some simple multipliers which take care of the age factor," of those between 60 and 80 years.

In this latest edition, moreover, Wechsler has completely revised the table of "signs" for different clinical entities revealed by the tests and has elaborated a new quantitative method for the determination of mental deterioration. These changes will render the book much more valuable to the clinician, both for his own records and in his interpretation of the results for the guidance of other members of the clinic in their final diagnosis and in the treatment and disposition of difficult cases. Alterations in the scoring of certain subtests and in the use of scores of subtests for further analysis of the mental deterioration or improvement of the subject constitute another improvement in the Scale. Further, the I.Q. range at the upper end of the Scale has been increased, "without, however, altering significantly the norms for the population as a whole."

Chapter 11, on Diagnostic and Clinical Features,

should be especially valuable, as it contains tables of test characteristics of the clinical groups, followed by comments on the groups and illustrative cases, each accompanied by a tabulation of the scores made on the subtests of both Verbal and Performance scales and the respective I.Q.'s.

In the standardization of the Bellevue Scale, the author found the following correlations with his criteria for validity: (1) Bellevue I.Q.'s and Stanford-Binet I.Q.'s: r = .82 ± .026; (2) with judges' (teachers') ratings, r = .43 and .52; (3) with psychiatrists' ratings of "recommended" or "not recommended" to commitment to a state institution for mental defectives, r = .79 ± .048 (in contrast with Binet I.Q.'s, where r = .33 ± .071). High correlations, empirically, existed with clinical criteria, such as: (1) social history; (2) comparative efficiency in verbal and performance tests, and in the latter versus vocational aptitude, motility, and ability to adjust to unfamiliar patterns of life; and (3) differentiation of general intelligence from educational disabilities. Of the 5000 subjects tested, only 3000 were used for the stanardization.

For three of the four measures of reliability generally used, the author got the following results: (1) S.E. of measurement for the Full Scale (I.Q.'s), whose mean and S.D. are, respectively, 100.11 and 14.69, is 5.674; (2) degree of correlation between the various portions of the same scale, 4 subtests x 4 subtests, r = .90 ± .014, and between verbal I.Q.'s x Performance I.Q.'s, r = .83 ± .018; (3) correlations between retests with the same subjects, children's r = .94 ± .013, adults' r = .94 ± .018.

In addition, correlations found by other investigators of the Full Scale with Stanford-Binet (1916 Revision) for various groups are: .57 ± .04, .81 ± .03, and .82 ± .03; with S-B, 1937 Rev., L, are .62 ± .04, .89 ± .01, .91 ± .02, and .93 ± .01. The two lowest r's, .57 and .62, are for college freshmen, both sexes combined and females, respectively. The remainder are for mental patients, (.89, .91, and .93), and for adolescent male delinquents, and adolescents aged 12–16.

In eight other studies, including the use of six different group tests of intelligence, the Bellevue Scale correlated from .39 ± .07 to .81 ± .04. Still other studies show correlations of various tests with the Bellevue Verbal Scale ranging from .48 to .92. Correlations of the Performance Scale with other scales are systematically, and often markedly, lower, than those of the Full Scale with other scales.

In view of the well adapted materials used and the evidences of standardization, validity, and reliability presented by the author, it seems that the new edition of the Bellevue Scale should prove to be highly reliable and valid for general use as well as for the special use intended with returning soldiers in the problems of their rehabilitation.

C. Hart Westbrook

Fear in Battle. *Fighting Forces Series.* *By John Dollard, with the assistance of Donald Horton. The Infantry Journal, Washington.* 25 cents (paper). v + 64 pp. 1944.

"This study of fear and courage under battle conditions is indebted first of all to 300 veterans of the Abraham Lincoln Brigade (volunteers for the service in the Civil War in Spain)...." "This group varied as to age, region, social status and political conviction. They had in common the belief that by volunteering they were fighting for democracy. Different as they may have been from a cross-section of the American army," they were hardened soldiers and had much in common. Their testimony "seems sensible and soldierly." "The typical informant was a rifleman, non-commissioned, poorly trained by American Army standards, wounded. All observers seem to agree that he was a tough fighting man." "The study bears only on the military experience of the informants...."

The several parts of the study deal with: Some Facts about Fear; Changes in Fear; Techniques of Fear Control; Fear and Morale; and Facts about the Report, including reliability, validity, errors of report, cause and identification with cause, and unconscious fear. The "Findings in Brief" are presented in 20 statements. These cannot be stated here for lack of space.

Each part is presented in a number of sections made up of summaries or generalized statements and occupying one page each; opposite each such page of facts or generalizations is an adequate graph of the percentages of the various statements.

The booklet will be of special interest to the psychologist as a study of one of the emotions, and should be of practical value to officers whose duty it is to train soldiers in the homeland or for service abroad. Perhaps it will be of most immediate value to officers and the men of the ranks themselves in the war areas of the world before, during, and after battle.

This study has blazed the path. Others should be carefully planned and pre-battle attitudes and fears discovered before the men go abroad; then continued with the men overseas, and, finally, carried to completion with men when they return on furlough and after they are discharged. The psychologists connected with the services, both at home and abroad, could do a fine piece of service in this way, calling in civilian psychologists to share the task with them here.

This is a very clear, interesting study of practical value, and it should stimulate much more research on the subject.

C. Hart Westbrook

Psychosomatic Medicine.

War Psychiatry.

Psychotherapy for Children. Group Psychotherapy.

Proceedings of the Second Brief Psychotherapy Council, Chicago, Illinois, January, 1944. Institute for Psychoanalysis, Chicago. 75 cents each; $2.00 a set (paper). 55 pp.; 64 pp.; 58 pp. 1944.

In the first of these three little volumes of proceedings, *Psychosomatic Medicine*, Alexander outlines the purposes and outlook of the Brief Psychotherapy Council. He defines the function of the Council as the bringing together of different investigators in order to afford an opportunity for exchange of views and experiences. He denies any rigidity of spirit in the organization, and while the Council operates under the Chicago Institute for Psychoanalysis, "it is no more representative of psychoanalysis than of group psychotherapy, psychodrama, hypnosis or narcosynthesis."

The contents of these volumes would give considerable support to this breadth of view. For example, the volume *Psychosomatic Medicine* contains an article by Barach on "Impairment in Emotional Control Produced Both by Lowering and Raising the Oxygen Pressure in the Atmosphere." Essentially a matter of research inspired by physiology, this contrasts with an article by Thomas M. French, "Brief Psychotherapy in Bronchial Asthma," which gives a beautifully stated summary of a case treated by Adelaide Johnson through analytic procedure with excellent results. Franz Alexander's study of hypoglycemic fatigue combines the physiologic and psychologic attacks on the problem. Weiss' paper on "Psychotherapy in Psychosomatic Disorders of the Gastro-intestinal Tract," and Daniels' on diabetes mellitus conclude this volume full of vivid experience vividly told.

The volume on *War Psychiatry* is equally good. A measure of the diversity of the attack on this matter is illustrated by the following titles: "Some Special Aspects of Psychotherapy in the Army Air Forces," by Murray; "Brief Psychotherapy in War Neuroses," by Grinker; "The Cornell Selectee Index," by Mittelmann; "Brief Psychotherapy in the Merchant Marine," by Blain; "The Use of the Multiple Choice Test (Rorschach) in the Military Services," by Harrower-Erickson. There is no particular point in singling out any one of these articles for special mention, since all are excellent. Grinker's statement concerning the war neuroses was very forcefully presented. Rado, in discussing Grinker's paper, pointed out that narcoanalysis had been used extensively in the last war, and that digestion of the traumatic experience even with this method does not guarantee the victim against recurrent difficulty. Rado claims that this can only be done by desensitizing the victim to trauma and training him in the psychological technique of handling himself in combat. He also pointed out that in World War I war neuroses, with a somewhat different symptomatology, it is true, were relieved much more quickly in large numbers by faradic shock in a proper atmosphere of suggestion.

In the third volume, divided into two parts, *Psychotherapy for Children* and *Group Psychotherapy*, there appear some very interesting papers. In the first part are Marian C. Putnam's description of "Psychotherapy in a Guidance Center for Infants and Pre-School Children"; Editha Sterba's "Brief Psychotherapy with Orthopedic Cases"; Liss' "Thrombocytopenic Purpura in a Case of Sado-masochism"; and Emmy Sylvester's "Emergency Psychotherapy of Pathologically Severe Feeding Disturbances in Children." This last paper may be singled out as an example of the shrewd use of intuition in dealing with what is always an exceedingly trying problem. The author states in detail exactly how she managed to develop rapport with a certain severely disturbed child and to achieve a resolution of the problem. This will well repay careful reading. In the second part, Redl describes the "Problems of Clinical Group Work with Children"; Lewis, "The Solution of a Chronic Conflict in Industry"; and Moreno, "A Case of Paranoia Treated Through Psychodrama."

These little booklets show that a great deal of effort is being made everywhere to break down the tremendous waste of time inherent in most methods of psychotherapy, a goal which one can only devoutly hope will be advanced along technically unassailable lines. When Alexander points out that a single contact with a patient may often produce as much good as a protracted analysis, he is only stating what the experienced psychiatrist has known for a long time. The question is how to organize information concerning pathology and therapy so that this goal can be more often reached.

WENDELL MUNCIE

CASE STUDIES IN THE PSYCHOPATHOLOGY OF CRIME. *A Reference Source for Research in Criminal Material. Volume Two.*

By Ben Karpman. Medical Science Press, Washington. $16.00. viii + 738 pp. 1944.

In this volume of some 738 pages Karpman has dragged out in detail the material, a considerable portion of which is autobiographical, on four criminals, the first convicted of theft of the U. S. mail and of drug addiction, the second of violation of the Mann Act, the third of rape, and the fourth of mail train robbery. This volume, in contrast to volume I of the series, has included some sexual crimes, whereas volume I dealt entirely with predatory crimes, and volume III, projected, is to deal with murder exclusively. This volume gives a great deal of material as the free association coming to light in psychoanalytic sessions, and one case, the second one, benefitted from the therapy through the discovery of a neurotic compulsive factor.

There may be some reasons which escape one for so extensive a presentation of such case material, but unfortunately it seems only long, tedious, and repetitious,

ith no special merit because it is in the victims' own rds. It seems that a much more effective presentaon would have been to give a concise statement of the se and extracts of the critical moments in treatment ched in the patient's and the physician's own words. is hard to believe that the careful, conscientious readg of any one of these four case histories will add very uch to the knowledge of causes, course, and treatment criminality in general. The first volume was likewise erburdened with words, with a dearth of concise lesns to be learned from it. The one case in the present oup, number two, which profited by psychotherapy rather interesting from that standpoint alone. The rusal of the case history also shows that there was a eat deal of wasted effort and time in the psychonalysis, and one may wonder if the same material ight not have been discovered with the same adantageous consequences to the patient by much mpler means. To put it briefly, this pretentious lume leaves one unconvinced of either the necessity r this kind of presentation or of any special results kely to accrue from it.

WENDELL MUNCIE

HUMAN BIOLOGY

TUDIES IN THE ANTHROPOLOGY OF OCEANIA AND ASIA *resented in Memory of Roland Burrage Dixon. apers of the Peabody Museum of American Archaeogy and Ethnology, Harvard University, Volume XX. Edited by Carleton S. Coon and James M. Andrews, IV. Published by the Museum, Cambridge, Mass.* $6.00 (cloth); $4.50 (paper). xiv + 220 pp.; 20 plates. 1943.

his collection of fourteen anthropological studies is resented in memory of Roland Burrage Dixon by a oup of his former students. Dixon was Professor of nthropology at Harvard University from 1915 to is death in 1934. The volume opens with a brief iographic sketch of Dixon and a complete bibliography his works. Nine of the contributions to this volume e devoted to ethnological and archeological subjects, amely: Polynesian Stone Remains, by K. P. Emory; etroglyphs in the Marquesas, by E. S. C. Handy; ods of Rennell Island, by G. MacGregor; Some Asects of Religion in Bougainville, by D. L. Oliver; ustralian Totemism, by R. L. Sharp; Culture Seences in Madagascar, by R. Linton; Certain Ancient urial Customs and Mortuary Objects from China, by . Chi; Observations on the Bronze Age in the Yenisei alley of Siberia, by J. H. Gaul; and a review of all ailable information regarding the Prehistory, rchaeology and Ethnography of Southern Arabia, by . S. Coon.

The remaining five papers deal with problems of ysical anthropology and as such are of particular terest to biologists. The first of these studies, by H. L. Shapiro, bears the title "Physical Differentiation in Polynesia," and leads to the following main conclusions: The Polynesian population shows a basic unity in its physical type and seems to have been derived from a fairly homogeneous ancestral stock in an as yet unknown area, which sent out successive and chronologically widely separated waves of invaders to all parts of Polynesia. The detailed physical differences among the present-day inhabitants of Polynesian islands may be due partly to local inbreeding or, more commonly, to the gradual differentiation in the original stock during the long period of emigration.

In another contribution, W. W. Howells discusses the Racial Elements of Melanesia, on the basis of our still very meagre knowledge of the physical anthropology of this region. Howells suggests that the first comers to Melanesia were Australian aborigines who had reached New Guinea, the Bismarck Archipelago, New Caledonia, and possibly a few other islands. The next immigrants were Negritos, who mixed with the Australians in New Guinea, but replaced them in New Britain, the Solomons, and the New Hebrides. The following arrivals, who probably came in many and long-continued invasions, were Negro peoples "resembling the typical Congo forest stock." These settled the lowlands of New Guinea, interbreeding with their predecessors, and extending their domain gradually to many of the other islands. Micronesian and Polynesian intrusions became superimposed later on and further complicated the racial composition of these regions.

In a paper on "Linguistic and Racial Aspects of the Munda Problem," G. T. Bowels reviews the information and theories concerning those isolated human groups in northern India who speak Munda languages, and he contributes many new observations on the physical characters of these people. The latter form a valuable and rare record; they are based on extensive series of individuals and contain accurate data for the most significant body measurements as well as for nonmetric features.

J. M. Andrews, IV, in an interesting essay on Evolutionary Trends in Body Build, makes use of his great collection of anthropological measurements on Siamese, as well as of certain findings by some other authors, to demonstrate lasting changes in human physique apparently resulting from environmental stimuli. In Siamese, Japanese immigrants of Hawaii, and New Englanders, who have changed their environmental conditions during one or more generations, body form has become altered in a strikingly similar manner. They have all acquired a greater stature and proportionately greater weight, and in addition there has occurred an increase in *relative* limb lengths and in *relative* shoulder and chest diameters, and a decrease in *relative* chest depth and hip breadth.

"Physical Types Among the Japanese" is the title of a paper by F. S. Hulse. Historical and ethnological

sources can tell us very little about the racial background of the Japanese, and archeological material, dating at most to the Neolithic period, is for Japan still scarce and inconclusive. The evidence uncovered so far indicates that the ancient inhabitants of the Japanese archipelago "apparently belonged to a branch of mankind sharing characteristics similar to those of the Australoid and to those of the Caucasian. This is also true of the living Ainu." After reviewing our inadequate knowledge of the physical anthropology of the recent Japanese population, the author presents some very welcome new data showing the morphological characters of living Japanese. Among the various existing types one can recognize some obviously pre-Mongoloid elements as well as those which lack Australoid or Caucasian features. Still other types possess in some respects a remarkable similarity to certain Chinese.

With these many notable studies on a wide variety of problems this memorial volume forms a very valuable addition to every anthropological library.

ADOLPH H. SCHULTZ

CHINA. *Smithsonian Institution War Background Studies Number Twenty.*

By A. G. Wenley and John A. Pope. Smithsonian Institution, Washington. 25 cents (paper). v + 85 pp. 1944.

This brief introduction to China is comprehensive and enlightening to a degree hard to believe attainable within a mere 85 pages. The first main section, on China's geography, follows Cressey on the whole, and concisely discusses the topography, climate, soil, agriculture, mineral resources, and populations of the land, region by region. Some of the figures for the populations of cities are not the most recent, and some are perhaps not good estimates at all, but sufficient warning is given about the unreliability of statistics on China. Wenley gives in eight pages a most illuminating account of the Chinese language, an account that could hardly be bettered in so brief a compass. Pope takes up China's history and foreign contacts, supplemented by an account by Wenley of China's part in the present war. Social organization and government are discussed by Wenley, with proper definition of the Chinese family and due emphasis upon its place in Chinese life. The section on Chinese art is especially good, as one would expect from members of the staff of the Freer Gallery. Pottery and porcelain, calligraphy and painting, bronze and other sorts of metal-working, and sculpture, together with minor arts and music all receive consideration. The final section, on the Chinese mind, is by Pope. Here Chinese philosophy, religion, and science are outlined, revealing, on the one hand, the great significance of tradition in the Chinese mind, and on the other, their genius for accepting foreign ideas and influences and amalgamating them with the older patterns of Chinese thought.

There is a brief, well-chosen bibliography but no index. Three useful charts of the periods and dynasties of Chinese history complete the pamphlet. The twenty-five plates of photographs are exceedingly good; and the seven maps, although lacking detail, are fairly helpful.

This little volume deserves the widest circulation among American citizens. It might very well, with others of the same series, serve as material for a new type of course in our high schools and colleges.

BENTLEY GLASS

PEOPLES OF SOUTHEAST ASIA.

By Bruno Lasker. Prepared under the auspices of the American Council of the Institute of Pacific Relations. Alfred A. Knopf, New York. $3.00. viii + 288 + x pp. 1944.

"The old relations between East and West were already in flux; crude exploitation and brute force have given way to principles of trusteeship, or guardianship, and of voluntary co-operation. The progressive application of these principles has been interrupted by the war. Now, the campaign of reconquest and the re-establishment of orderly rule provide a unique historical occasion. Here is the chance, in one of the world's most important culture areas, to do something more than just continue where we left off." In the pages that follow this introductory statement, the author discusses the problems, injustices, and general unrest that exist within the region, and demonstrates the need of a concerted effort on the part of the rest of the world to do something to alleviate the underlying causes. The fundamental aim of this book is to furnish the reader with authoritative information on existing conditions in order that he might more intelligently deal with these problems.

This region of islands, peninsulas, seas, swamps, and fertile soil is the home of an estimated one-fifteenth of the world's population. The native inhabitants belong to a wide variety of social groups ranging from head-hunters to skilled artisans and cultivators of commercial crops. The author does much to dispel the general belief that these peoples of the Asiatic tropics are fundamentally inferior. Their apparent laziness and their willingness to use outmoded methods of agriculture is explained on the basis that they have not been convinced that greater industry and agricultural output furnishes adequate reward. Their lack of thriftiness is accredited to the fact that it is to the interest of certain groups that they fall into debt. We are reminded that these tropics have given the world some of the oldest civilizations. As evidence the author mentions the lofty and intricate Hindu structures recently discovered in Cambodia and Java, the Polynesian sea-

farers who conquered great distances in the Pacific long before Columbus succeeded in crossing the Atlantic, and the Malay and Arab mariners that linked China and Imperial Rome in trade. The inventiveness of the natives is also emphasized, and we are told that it was the Malay who taught us how to build the suspension bridge. The reader is shown that the region and the inhabitants have inherent potentialities that, if given opportunity and proper guidance, are capable of contributing much to civilization today.

In spite of the evils of the colonial system that has exploited the region for foreign interests, it has accelerated the progressive advance from lower to higher levels of civilization. Unfortunately, in many instances this has only given them a glimpse of a better life that they are unable to attain, and tastes which they cannot gratify. Although the Netherlands' government has done far more than the British for their subjects, neither has done enough to assure the natives that their position is to improve fundamentally. This has caused a contagious "oppression psychosis" to spread throughout the region. The people are conscious of their poverty and the restrictions that make it impossible for them to obtain what they now desire. "We are told that, even though the native cannot buy the same degree of physical and mental efficiency as the Occidental, he is happier in his native civilization. An enthusiast of the simple life—for others—may even add that the native is happy in proportion to his lack of contact with Western life and his ignorance of its paraphernalia. There might be something to this—though I doubt it, as everybody must who knows the perils and fears of primitive life—yet those who use that argument do not in the least intend that the carriers of Occidental civilization should move out and leave the natives a free field." Since the Occidentals are not willing to "move out," it is important that they relieve the troubled conditions. The author believes this can be done by a gradual change to self-rule through education and training for leadership; by encouraging and developing native industries; and by improving the agricultural and economic systems. In other words, the mother countries and their representatives should serve as trustees in the development of Southeast Asia rather than exploit the region to their own advantage.

The book is not a particularly readable one. This may be due in part to the frequent use of long sentences that are held together with many commas, semicolons, and dashes. Nevertheless, it is well worth the time and effort for the valuable material that it presents.

M. M. BROOKE

OLD ORAIBI. *A Study of the Hopi Indians of Third Mesa. Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University, Volume XXII, Number One.*

By Mischa Titiev. Published by the Museum, Cambridge, Mass. $4.50 (paper). xi + 277 pp.; 4 plates. 1944.

In the field studies that form the basis of this monograph, the author has concentrated on two aspects of Hopi culture: social organization, and ceremonialism. He discusses these two items in the first two parts of his excellent book, while a third part (miscellany) and an appendix contain, besides an important chapter on "the economic background," mainly additional material on ceremonialism. The author has always integrated his own findings into the considerable body of existing material dealing with Hopi and Pueblo culture.

Titiev's handling of the data on "Kinship and Social Organization" is particularly praiseworthy, all the more since kinship data, ever since the evolutionary approach was given up, have been rather dead-weight in so many anthropological monographs of the past. Titiev gives not only a more detailed and correct description of kinship data than his predecessors; he also uses the more modern functional approach of supplementing mere kinship nomenclature by data on the reciprocal behavior of kindred. In analysing the split of Old Oraibi in 1906 into three villages, he shows the inherent tendency of Hopi social organization towards such developments, and is thus able to throw new light on the old and puzzling question why the Pueblo archeologist finds so many abandoned village sites. When Titiev reduces the three old explanations of this phenomenon —war, climate, and disease—to their true proportions, he makes an important contribution toward a necessary general revision of our opinions concerning the *primary* historical rôle of at least the last two factors. Climatic and pathological explanations of historical events have been used very widely and very loosely during the last few decades, only to crumble every time the respective problem has been examined in detail and in all its ramifications.

Titiev tries to give not only a description, but also a deeper understanding of the extremely complicated and varied ceremonialism of the Hopis in abstracting the fundamental ideas underlying the numerous rites, ideas which find expression also in the Hopi calendar. The most important point seems to be that where we see life and death as two opposed categories, the Hopis see only one whole composed of two life cycles, one in the upper, one in the lower world, supplementing each other. This supernatural extension of their life sphere, re-enacted in their rites, supplies the Hopis with the all-important assurance that in spite of a hostile environment, they cannot be destroyed.

ERWIN H. ACKERKNECHT

NAVAHO WITCHCRAFT. *Papers of the Peabody Museum of American Archaeology and Ethnology, Harvard University. Volume XXII, Number Two.*

By Clyde Kluckhohn. Published by the Museum, Cambridge, Mass. \$2.25 (paper). x + 149 pp. 1944.

During the last sixty years a great body of excellent information concerning Navaho food, Navaho techniques (blankets, silver-work), and Navaho religion and its ceremonials (chants, sandpainting) has been collected. Yet almost no attention has been paid to what the Navahos themselves refer to as the "bad side" of their supernatural techniques and beliefs. This is largely explained by the fact that information on witchcraft, the greatest of all crimes, is very difficult to obtain in Navaho as well as in most other primitive cultures. Only an ethnographer extremely familiar with Navaho folkways and the Navahos themselves, such as Kluckhohn, could fill this essential gap in our knowledge and understanding of Navaho culture. The merits of Kluckhohn's monograph are not limited to the rather narrow field of "Navahology." His intelligent discussion of one particular case of witchcraft contributes essentially to a better understanding of the whole phenomenon, which seems to be connected with a certain "paranoid" attitude, one of the basic traits of human mentality, collective and individual. The author himself alludes to such larger implications, calling the Navaho belief in witchcraft a "substitute for race prejudice."

In a descriptive part, Kluckhohn formulates the different forms of witchcraft belief, as he found them among the Navahos. A large part of the raw material from which this part is abstracted is given as an appendix. In an interpretative part, he emphasizes the relatively limited disruptive consequences of witchcraft in this given culture, the increase of witchcraft beliefs in periods of heightened socio-economic tension, and the functional rôle which witchcraft plays in Navaho society. Though at a high cost, the witchcraft belief provides at least certain legitimate ways to display anxiety and aggression. It has a certain controlling effect upon the rich, and the powerful singer, a certain protective value for the destitute. It provides an explanation for a number of startling phenomena. From witchcraft beliefs, certain conclusions can be drawn as to objective and subjective situations in Navaho life, productive of strains and stresses.

E. H. ACKERKNECHT

THE ABORIGINAL CULTURE OF THE CÁHITA INDIANS. *Ibero-Americana: 19.*

By Ralph L. Beals. University of California Press, Berkeley and Los Angeles. \$1.25 (paper). x + 93 pp. 1943.

The Cáhitas are a complex of closely related Indian tribes living near the Mexican border between the states of Sonora and Sinaloa. They are much alike in all phases of their culture except language. This fact was observed by the Jesuit missionaries of the sixteenth century who found that every time they crossed a watershed they were obliged to learn a new idiom.

This fact would seem to indicate that travel was not a luxury in which the Cáhitas indulged. And no wonder! Water, the most indispensible requisite for the support of any kind of life, is notoriously scarce on the shores of the Vermilion Sea. In midsummer there may be cloudbursts in the mountains and then the rivers may rise, traversing their channels with such violence that a crossing is impossible without danger to life and limb; then the waters subside as quickly as they rose, and the stream bed again becomes a desiccated arroyo from which water may be obtained only by digging. The Indian dares not travel far from the water which not only supports his own life, but upon which he has learned to depend for irrigation of his crops as well.

The author of this work learned by experience that each tribe of Indians was acquainted with the contiguous tribes, but could tell him nothing about those living at more remote distances, another fact which testifies of the extent to which the Indians are fettered to the soil.

This work is not indexed, but its table of contents is detailed, and the material is so systematically organized that the lack of an index is not a serious defect. Every phase of the cultural life of the Indians is abundantly covered. First the elemental needs of food, clothing, and shelter are discussed; then the social, industrial, and political details of their life, with such other subjects as their use of tobacco, their recreations, and their religious ceremonies are taken up in order. The work is well illustrated by both plates and text figures, and there are tables setting out certain meteorological data.

The only adverse criticism that the reviewer might make of this study is the omission of any mention of the two most interesting tribes from this area. Probably neither one is Cáhita. The first of them is the Seri tribe, whose native habitat is on Tiburon Island, but who have recently migrated to the mainland to take advantage of the pecuniary opportunity afforded by the fishing industry. When the Spaniards discovered the Gulf of California, the Seris were living in a neolithic culture, and as late as the end of the nineteenth century they occasionally indulged in "long pig."

The other tribe is that of the mysterious blond Indians from the valley of the Yaqui River. Rumors of blond Indians are nothing new; they are at least as old as the time of Balboa and occur everywhere from the Orinoco to Baffin Bay, but the report of blond Yaquis seems to rest on better evidence than most of them. President Alvaro Obregon had red hair, a fact which accounted for the now discredited belief that the original form of his patronymic was "O'Brian"; and Cajeme, the chieftain who successfully defied Porfirio Diaz, and who is claimed by both the Yaquis and the Mayos, is said to have had yellow hair and blue eyes. Cajeme has not been dead long enough to have become

a tradition—he is remembered by people now living—and it ought not to be difficult to check up on his complexion. It is important that this be done before it is too late, as a recent author reports a Seri tradition of a mysterious ship, manned by tall blue-eyed sailors who spent a winter at Kino Bay harpooning whales and boiling their blubber in caldrons long before the visit of Francisco Ulloa to these shores. From this the author concludes that the blood of the Norsemen flowed in the veins of Cajeme, and that his blond complexion was a heritage from this ancestry. Speculations of this nature may appeal to one's sense of the romantic but should not be accepted unless based on convincing evidence, and it is unfortunate that the author did not include the blond Indians in his survey so that he might have either confirmed or denied their existence authoritatively.

SOME EARLY SITES IN THE NORTHERN LAKE TITICACA BASIN. *Peabody Museum of American Archaeology and Ethnology, Harvard University. Volume XXVII, Number One.*

By Alfred Kidder, II. Published by the Museum, Cambridge, Mass. $1.25 (paper). vii + 48 pp.; 7 plates. 1943.

ARCHEOLOGICAL REGIONS OF COLOMBIA: A CERAMIC SURVEY. *By Wendell C. Bennett.*

EXCAVATIONS IN THE VICINITY OF CALI, COLOMBIA. *By James A. Ford.*

Yale University Publications in Anthropology, Numbers Thirty and Thirty-One. Yale University Press, New Haven; Oxford University Press, London. $2.50 (paper). No. 30, 120 pp.; 12 plates. No. 31, 79 pp.; 4 plates. 1944.

PERUVIAN ARCHAEOLOGY IN 1942. *Viking Fund Publications in Anthropology Number Four.*

By A. L. Kroeber. The Viking Fund, Inc., New York. $3.00 (paper). 152 pp.; 48 plates. 1944.

Between the archeology of the New World and that of the Old there is a great gulf fixed. Upwards of three millennia ago the Phoenicians had perfected a system of phonetic writing, while the inhabitants of the plateaus of Anahuac and Tiahuanaco, despite the relatively high degree of civilization which they had achieved at the time of the conquest, still had to have recourse to a system of hieroglyphics comparable to that of the early dynastic periods of Egypt. Our knowledge of the early civilizations of the Mediterranean basin comes largely through the Rosettta Stone, upon which is incised the same text in hieroglyphic, hieratic, and phonetic scripts; but there can be no Rosetta Stone to help us unravel the megalithic inscriptions of Yucatan or the mnemonic quipus of Cuzco and the Titicaca region.

In the Old World, history and archeology have joined hands, and in what they reveal to us of the glory that was Greece and the grandeur that was Rome we can recognize the handiwork of our own intellectual ancestors in the Parthenon and the Coliseum. But the builders of the pyramid of Tenayuca and the serpent mound in southern Ohio are forever surrounded by a screen of impenetrable mystery, and we can know no more of them than did Shelley of Ozymandias. For this reason even the most scholarly reports of American archeological investigations contain little to stir the imagination. There is nothing among them comparable to Schliemann's discovery of the site of Troy, or Carter's excavation of the tomb of Tut-ankh-amen. Even the gold artifacts of Monte Alban, sensational as they were when first announced, have been largely forgotten today because they could not be connected to anything that seems familiar to us.

The three works under discussion here consist largely of inventories of potsherds, with annotations as to whether or not they were colored or glazed, whether or not they had handles, what purposes they might have served, etc. Such data, while undoubtedly of importance to the specialist, are likely to have but little interest to the more catholic devotee of archeology. They are significant partly because potsherds are frequently the only remaining evidences of vanished cultures, and partly because they may reflect differences among separate cultures.

But those who wish more dramatic evidence of vanished peoples may find them in the architectural remains uncovered in the Andean highlands. In the Titicaca basin the Peabody Museum has excavated a temple of astonishing size, the foundation of which consists of rectangular blocks of stone approximately 8 x 3 x 2 feet in size. It is the most complex edifice yet discovered in the region, though it may be surpassed in future investigations.

At San Augustín, in western Colombia, a Yale University expedition has uncovered a quantity of carved rocks. Some of these appear to be boulders, and mark the site of tombs, but others are part of the bedrock and are still *in situ*. Some of these carvings represent animals, and others are geometrical designs. The people who carved them were also expert goldsmiths, if one is to judge by the illustrations of gold artifacts from the same locality, now in the museum at Medellín.

But to the reviewer the most interesting feature of any of these expeditions is the wooden "Stonehenge" at La Estaquería in southern Peru. This structure, which has never been illustrated before, so far as the author is aware, consists of a multitude of trunks of algarroba trees set up vertically over an area of approximately 800 square meters. Algarroba wood is extremely tough and durable, and has been used for lintels in stone walls of undoubted pre-Hispanic origin, for which reason the author suggests that these wooden steles would afford an excellent opportunity for a tree-ring study. This is especially true because living algarroba trees are readily available nearby for comparison.

All three reports are extremely well prepared, and the plates, some of which are photographs and some drawings, are among the best that this reviewer has ever seen. The reports are thoroughly indexed, and excellent examples of what such reports ought to be. That dealing with Colombia has an introduction, dealing with the geography of the area, which makes intensely interesting reading.

THE AMERICAN CHARACTER.
By Margaret Mead. Penguin Books (Pelican Books), Harmondsworth and New York. 9d (paper). 173 pp. 1944.

Two-thirds of this book is devoted to an analysis of the American character, the author taking her clues from the way young Americans are raised. Her result is the following:

"We have a certain kind of character, the American character, which has developed in the New World and taken a shape all its own; a character that is geared to success and to movement, invigorated by obstacles and difficulties, but plunged into guilt and despair by catastrophic failure or a wholesale alteration in the upward and onward pace; a character in which aggressiveness is uncertain and undefined, to which readiness to fight anyone who starts a fight and unreadiness to engage in violence have both been held up as virtues; a character which measures its successes and failures only against near contemporaries and engages in various quantitative devices for reducing every contemporary to its own stature; a character which sees success as the reward of virtue and failure as the stigma for not being good enough; a character which is uninterested in the past, except when ancestry can be used to make points against other people in the success game; a character oriented towards an unknown future, ambivalent towards other cultures, which are regarded with a sense of inferiority as more coherent than our own and with a sense of superiority because newcomers in America display the strongest mark of other cultural membership in the form of foreignness."

The author analyses the American character for a specific purpose: to find out in which way the maximum energies of this given character can be mobilized for winning the war. In the last third of her book, Mead develops the goal that in her mind would release this maximum energy: a new synthetic world culture, engineered by Americans on the basis of the "peculiar blend of moral purpose and practical inventiveness" that makes up the American character.

Though Mead's highly interesting book (which was published in this country two years ago under the title *And Keep Your Powder Dry*) deserves detailed discussion, this journal seems not to be the place for it. Though probably not inferior in quality to the author's former publications, which have made her one of the leading anthropologists of our time, this highly emotional book is definitely of a different quality, as it is built on premises and pursues goals which are not those of scientific treatises.

ERWIN H. ACKERKNECHT

FOOD ENOUGH. *Science for War and Peace Series. By John D. Black. The Jaques Cattell Press, Lancaster, Pa.* $2.50. vii + 269 pp. 1943.

Black, professor of economics at Harvard University, in this book sets forth clear, pointed arguments relating to the necessity for the production and effective distribution of "every possible pound of human food" at the present time. The food needs of the armed forces, of war workers and other civilians, of our allies, via Lend-lease and UNRRA, are plotted on the basis of realistic postulates and the most recent statistics. Germany's food picture is also surveyed and found to be not too great a weakness in her military situation. Consideration of problems of production resulting from the manpower situation, from the lack of farm machinery, from the needs for non-food crops, and from the relation between what we need, what we could produce, and what we can afford all lead up to the question of desirable shifts in production and consumption. The program Black outlines calls for less meat and more milk, eggs, peas, beans, peanuts, and soybeans; less animal fat and more vegetable oils; more potatoes; and tomatoes, carrots, and other vegetables and fruits that can be produced with relatively little labor instead of those that require a lot. In discussing food prices and rationing and the general problem of distribution, Black pulls no punches in criticizing past and present policies and practices. He ends by summarizing the program of the United Nations Food Conference of 1943 to achieve world-wide freedom from hunger, and by discussing the necessary elements of international cooperation in this field.

This is an excellent treatment of the interrelations of nutrition, agriculture, economics, and human relations in the current situation, written for the layman in non-technical style. The only obvious criticism—one beyond the author's control—is that events have moved so rapidly and conditions have altered so markedly since August, 1943, that much of the program will already need modification. The main points, however, will not have altered. In-plant feeding will still be desirable for war workers; soybeans will still be needed as never before; civilians should still make shift with less meat; and more thought and careful planning will be required before the world's hunger is stilled.

BENTLEY GLASS

ON LIVING IN A REVOLUTION.
By Julian Huxley. Harper and Brothers, New York and London. $2.50. xiv + 242 pp. 1944.

This collection of essays is assembled, with a few new offerings, from magazine articles published during the war years. Certain of them bear directly on Huxley's views of the world situation today. Briefly: we are experiencing, in the war, one symptom of a world revolution. The inevitable trends of this revolution are, within nations, toward the subordination of economic to non-economic motives, toward more planning and a more conscious social purpose; internationally, toward greater organization and a fuller utilization of the resources of backward countries. The revolution may assume either a democratic or a totalitarian form, the latter being self-defeating in the end. The only universal mark of democracy is the satisfaction of the needs of individuals, their welfare, development, and active participation in social processes, and eventually their equal cooperation in international organization. The revolution, like the war, must involve our conscious acceptance and participation, in either a democratic or a totalitarian way. These ideas are set forth in the first essay, reasserted in the second, and reiterated in the third, with echoes and reverberations in the majority of the remainder. Notwithstanding general agreement with Huxley's point of view, one could wish that repetition had not been carried to the point of diminishing returns. However, in some of the essays, such as "Colonies in a Changing World" and "Reconstruction and Peace," these views are applied to the solution of postwar problems; and definitely new ground is broken in "Education as a Social Function," in which Huxley calls for the application of scientific treatment to education and suggests the need for adapting it to social trends.

Biologists will find most pertinent the essays on "War as a Biological Phenomenon" and "Darwinism Today." These are excellent summaries of subjects developed at greater length in *Evolution: the Modern Synthesis*. "Philosophy in a World at War" represents Huxley's matured monistic philosophy, which places man at the end of the line of evolutionary progress, one who "stands alone as the agent of his fate and the trustee of progress for life." These ideas, also, Huxley has amplified in the magnum opus referred to above and in *Man Stands Alone*. The essay on "'Race' in Europe" is a digest of *We Europeans*. "Birds and Men on St. Kilda" and "Animal Pests in Wartime" are very interesting studies of man's relations to animal populations.

Altogether, while one familiar with Huxley's work will find here little that is wholly new, there is vigor and a modicum of fresh thought that is stimulating, and as a summary of Huxley's thinking the collection is valuable. And everyone, I am sure, will enjoy Dr. Spooner, who somehow, in his characteristic way, wandered irrelevantly into this book.

BENTLEY GLASS

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SCIENCE AND CRITICISM: *The Humanistic Tradition in Contemporary Thought.*

By Herbert J. Muller. Yale University Press, New Haven. $3.75. xiv + 303 pp. 1943.

A more or less satisfactory compendium of achievements in one or more of the sciences is easily found. The desire on the part of some scientists to have their work more widely understood, and the desire of many laymen to find some reassurance through comprehending the very real achievements of science, take care of this.

Herbert J. Muller has also set out to further the general understanding of modern science, but his book has more than usual value because it is written with a rather specific purpose.

In the first place, he considers not the concrete achievements, but the current theoretical concepts of physics, biology, psychology, and the social sciences. These concepts, conflicting and controversial as they are, often providing fields for acrimonious debate and undebatable prejudice, he has reviewed with a rare combination of critical judgment and sympathy.

The second distinguishing feature of *Science and Criticism* is that it was written for the critic. It is designed to show him how the theories and attitudes of modern science can contribute to his work of criticism. This aim leads to a statement of the outlook of scientific humanism, its relevance to the present day situation, and its value for the critic.

One does not have to enquire into the author's qualifications as an interpreter of science. His treatment of the material is evidence enough of his ability to seek and evaluate without arbitrary judgment, whether in applause or condemnation.

Science and Criticism is intended primarily for the literary critic; but inasmuch as we are all critics, of life if not of literature, it will have a very general interest and use.

EILEEN SUTTON GERSH

A SHORTER HISTORY OF SCIENCE.

By Sir William Cecil Dampier (formerly Whethem). Cambridge: at the University Press; The Macmillan Company, New York. $2.00. x + 189 pp. 1944.

This meaty little volume is a masterly condensation of the author's *History of Science*. It is designed for the benefit of "older schoolboys" and the "general reader." The sections dealing with the philosophical and religious implications of science have been drastically cut, although the reader is always made aware that science is no mere bag of technological tricks. Following the tradition of his great predecessor, Whewell, at Trinity College, Cambridge, Dampier has given the physical sciences a central place, which is as it should be in a

general history. This story of the development of the physical sciences is told with a force, comprehensiveness, and insight that are unmatched in the English language. The focus is held steadily on the great themes—stars and atoms, matter and force—but the mass of lesser topics is prodigious, skillfully organized, and ranges all the way from dynamos to Robinson Crusoe.

Undoubtedly the weakest part of the book is that concerned with the biological sciences. The eugenical and sociological views that crop out in several places can only be called a minor scandal. It may be that Rome fell because the purity of its blood had been corrupted by foreign elements. It may be that the old landed families of England have more genes for great scientific ability than any other group in the population. We would only ask, in the broken English of a distinguished American physiologist, "Vot iss de effidence?" The explanation of such statements seems to be simply that the author has been so caught up with the rush of discovery in the physical sciences that he has not had the time to reinvestigate such questions since his own work in 1909. The eugenics is scarcely Galtonian. It seems incredible today that no distinction should be made between chromosomal and cultural inheritance. The anthropology is mostly Frazer's *Golden Bough*. Malinowski is not even mentioned in the index.

Several common errors have crept in. Schleiden and Schwann are credited with the cell theory and specifically with having traced the cells back to their origins in the embryo. The relative space given to various biological topics and individual investigators is sometimes surprising. Pasteur's biological work fills three lines. Lady Mary Wortley Montagu receives slightly more.

It has been suggested that this little book is perhaps too condensed for the general reader or for school use. However, in any book that is to be kept down to a reasonable size, the actual choice is not between a condensed mention and a full explanation but between a mention and nothing. We are convinced that far better results are achieved both in stimulating interest and in imparting the truth by at least telling the boys, as Dampier does, that after some two thousand years Lobatchevsky has succeeded in seeing through Euclid, and Cantor in resolving the paradoxes of Zeno, then by silently implying that Euclid and Zeno have said the last word. Of course, the only scientific way to determine how useful this book will be for the older schoolboy is to try it on him in statistically significant numbers and find out.

G. B. MOMENT

MEN OF SCIENCE IN AMERICA. *The Role of Science in the Growth of Our Country.* *By Bernard Jaffe. Simon and Schuster, New York.* $3.75. xi + 600 pp. 1944.

Slightly over ten years ago I found Jaffe's book *Crucibles* intensely interesting, helping to make real to me some of those chemists previously only names in books. I therefore picked up his widely heralded new book on American science and scientists with keen anticipation. It must be set down, however, as disappointing in some respects although excellent in others.

The general plan, that of weaving the entire history of American science around certain outstanding figures in a variety of fields, is well conceived. The effort to show the influence of their times on these men, and their reactions to political, social, and economic problems is consistent, if at times, perhaps, rather overstrained. The choice of central figures is very good, and equally representative of the physical and biological sciences, only psychology having been ignored. The list begins with Thomas Harriot, early naturalist and mathematician, and passes chronologically to Franklin, Benjamin Thompson, Thomas Cooper, Rafinesque, Say, Morton, Henry, Maury, Agassiz, Dana, Marsh, and Gibbs in the nineteenth, and Langley, Michelson, T. H. Morgan, Herbert M. Evans, E. P. Hubble, and E. O. Lawrence in the present century, making eleven men in the physical sciences and eight in the biological. This is preeminently a list of workers in "pure" science, not in invention or applied science. No two writers, perhaps, would pick out exactly the same group of scientists, and Jaffe's choice is certainly thoughtful and well balanced. The accounts are vivid and abound in anecdote and interesting detail. The plates supply good portraits of the central figures.

On the other hand, Jaffe's style has not improved with the years. There are too many pronouns of dubious antecedents; too many misused words; too many unhappy expressions. The organization of material within the individual chapters does not appear to have been so carefully planned as the larger organization of the book; the chronological pattern tends to become obscured by abrupt transitions back and forth.

In the chapter on Thomas Hunt Morgan and the rise of American genetics more serious defects are to be found. It is amply evident that, however lucid and accurate his discussions of physical science may be, Jaffe is not at home in the intricacies of genetic principles. There are many minor slips that may be apparent only to geneticists and do not affect the thread of the story. However, when Jaffe comes to relate how Mrs. Morgan discovered the flies with attached-X chromosomes, he becomes utterly confused. The attached-X females are metamorphosed into gynandromorphs (one is even illustrated), and Mrs. Morgan is said to have "bred thousands of this queer intersex race of flies, crossbred them, interbred them," and more similar nonsense. A little farther on, Muller is said to have "actually transmuted species and created new ones by exposing flies to the action of ordinary X-rays!"—a remark that

will certainly cause him distress. The whole fabric of confidence in a writer's carefulness and accuracy is so undermined by this tissue of errors that one would be tempted to condemn the entire book, were it not that in the next chapter Jaffe does a creditable piece of reporting on the research upon hormones and vitamins. A biologist may assume that the accuracy of the other sections is probably fairly high and excuse Jaffe on the ground that he is not the first to err egregiously when trying to write about genetics.

This is a stimulating book in spite of its glaring defects. It presents a comprehensive view of the growth of American science that fills a real gap in our accounts of the development of science.

BENTLEY GLASS

SCIENCE IN THE UNIVERSITY.

By Members of the Faculties of the University of California. University of California Press, Berkeley and Los Angeles. $3.75. x + 332 pp. 1944.

It is an unexpected pleasure, in these days of cheaply produced wartime books printed on inferior paper, to pick up a really excellent example of book-making such as this volume celebrating the Seventy-fifth Anniversary of the founding of the University of California. One can only wonder how the publishers managed to do it.

The contents include nineteen essays by members of the faculty, each presenting a picture of a limited part of the scientific research that has made the University of California, from its earliest days, a leader in this respect. The articles are varied not only in content but also in style and purpose, having in common chiefly their aim to create unitedly a panorama of interesting research that will inform fellow scientists and educated laymen of the achievements of research in the institution. Some few articles are so technical that they will be appreciated only by specialists in the author's field. Others are written in simple and non-technical language for every citizen to read. The majority fall in between.

Robert Grant Aitken summarizes first the general development of astronomy from the time of Galileo. J. R. Oppenheimer covers the progress of the study of cosmic radiation since 1936. The discussion of molecular forces and solubility, by J. H. Hildebrand, is exceptionally illuminating, and biologists will find it well worth their while to read it. The contribution of Carl L. A. Schmidt on the chemistry of the amino acids and proteins is only too brief. A survey of the history of organic chemistry, by G. Ross Robertson, emphasizes rather more than do the previous essays the contributions of Californian science.

Jakob Bjerknes provides a clear account of the factors involved in the rise and fall of barometric pressure, and H. U. Sverdrup of the Scripps Institute of Oceanography writes on the California current, a subject that will especially interest ecologists. Wm. C. Putnam's account of the geological evolution of the Mono Basin during the Pleistocene is very interesting. One wonders why, in so richly illustrated a book, he did not include at least a few photographs of this Sierran landscape. U. S. Grant IV discusses the more technical topic of the causes and amounts of subsidence and elevation in the Los Angeles area in recent years, some of the subsidence being man-made.

The biological contributions begin with a very general essay by O. L. Sponsler on modern conceptions of protoplasm. Richard Goldschmidt follows this with a review of the evidence that has led him to regard genetic changes as resulting from rearrangements of chromosome material and to dispense with the older idea of gene units. Geneticists will find this controversial matter interesting, but to others it will no doubt seem the most technical article in the volume. The late C. B. Lipman has vividly described his long-continued experiments on the survival of bacterial spores in centuries-old mud bricks from California and Peru. Claude ZoBell, of the Scripps Institute, writes on the relation of the study of the sea to man. Ralph Chaney, in a beautifully illustrated article, considers the paleobotany of California; and L. Miller, the recent evolution of California's birds. D. R. Hoagland's treatment of general aspects of the study of plant nutrition is excellent. J. M. D. Olmsted writes on the place of physiology as an independent science, Knight Dunlap on the contributions of psychology, and S. J. Holmes concludes the volume with an essay on evolutionary ethics. The latter is a penetrating criticism of Thomas Henry Huxley's Romanes lecture of 1893, and comes to much the same conclusions about the origin of ethical values as those recently published by Julian Huxley. The contribution by Dunlap is marred by dogmatic statements and a general tendency to attribute his own views to all psychologists. Geneticists will be astonished at the view he expresses that about hereditary traits nothing can be done, and that heredity is not among the real (sic!) causes of traits. Nevertheless the article is stimulating and presents a valuable survey of recent trends in psychology.

All in all, the University of California has ample reason to congratulate itself in being so well presented to both scientific and lay publics in this volume.

BENTLEY GLASS

ALASKA DIARY 1926–1941.

By Ales Hrdlicka. The Jacques Cattell Press, Lancaster, Pa. $5.00. xv + 414 pp. 1943.

During his trips of exploration it was the custom of the author to record, aside from his scientific work, daily notes of current events and experiences. It is these notes of his 1926–1941 expeditions to Alaska which have been gathered together in the present volume.

They are, as Doctor Hrdlicka states in his preface, "just brief but faithful records of what befell or was encountered by the writer and his coworkers in those far-away and lonesome, yet scientifically important regions, in quest of anthropological information." As is to be expected, such notes contain numerous items that are more or less relevant and complementary to the scientific results proper which have been published elsewhere.

Throughout the records, considerable attention has been given to the weather, to food, and to transportation, for, as the author points out, these factors are constantly with one in the Far Northwest and not seldom prove of paramount importance. They can thwart or make very difficult the best laid plans or again facilitate them. "Mind, health and physical strength, however necessary, are alone often powerless in these parts. Man is here against the elements, against want of things and means, and must repeatedly give way." Often the brief sentences (almost telegraphic in style) reflect the suffering from the hardships of the days—the cold rains, the storms, the weariness of effort, the lack of facilities, the pests of mosquitoes and gnats. But there is also a brighter side. As to illness, we are told that "there is something strange and most grateful in this respect in Alaska." Apparently there is an actual absence of many of the common viruses and bacteria. Wholesome hunger never fails and all digestive troubles vanish. "What would many a city dweller give for the Alaska hunger—with the dreamless refreshing nights; and the rest of us for the pure cool Alaska water." The water, we are told, is mostly so good that one grows almost addicted to it! The mountain scenery is superb, and for the anthropologist there is always the constant tonic of new discoveries.

The ten seasons, in all, spent in Alaska by the author have thrown substantial new lights on the problems of the peopling of America. Where before there was but a haze of opinion, there are now definite facts substantiated by large collections. Nearly 4,000 crania and skeletons have been collected or excavated and have afforded a solid basis for important conclusions. The present text shows how many of these collections were made and what, in general, they embrace. So far, what the work has made possible, we are told, is the recognition of the archeological riches of the region; of the direct connection of these remains and their people with Asia; of the presence of hitherto unsuspected old human strains in the territory; of the high material cultural status of the occupants of the region in prehistoric times; and of its connections anthropological as well as archeological, with the rest of continental America. While much has been accomplished there is yet much to be done. According to the author, there is enough left in Alaska to occupy American anthropologists and archeologists for generations to come, and to give a wealth of additional materials.

The text is abundantly illustrated with some 200 photographs which in themselves are extremely interesting. The volume is also well indexed.

MEET MR. GRIZZLY. *A Saga on the Passing of the Grizzly.*

By Montague Stevens. The University of New Mexico Press, Albuquerque. $3.50. x + 281 pp. 1943.

This is a book for sportsmen who will be delighted with these highly entertaining, rambling memoirs of the author, an old English gentleman who became a rancher in western New Mexico some sixty years ago. The accounts of hunting and of training dogs and horses contain much that is original and informative, and the thrilling advantures with animals and men are well worth reading. The author assembled and trained with exceptional care effective packs of dogs for trailing and fighting bears, and succeeded in killing numerous black and grizzly bears.

The naturalist and the psychologist can find among these reminiscences unusual and detailed observations on animal behavior, although, in spite of the title, there is much more pertaining to dogs, horses, and men than to bears. Of greatest interest are the lengthy descriptions of the remarkable accomplishments of bloodhounds in trailing man and beast, and of the author's success in making his hounds comprehend what is expected of them. The nature of the grizzly bear is not as fully depicted in the present volume as it has been in various other publications, particularly in that great old book by W. H. Wright, *The Grizzly Bear* (New York, 1909).

EMULSION TECHNOLOGY, *Theoretical and Applied, Including the Symposium on Technical Aspects of Emulsions.*

Edited by H. Bennett. Chemical Publishing Company, Brooklyn. $5.00. xi + 290 pp. 1943.

This book contains the twelve papers originally published by the same publishers in 1935 under the title *Technical Aspects of Emulsions.* This was a collection of papers read at a symposium held in London on December 7, 1934, by the British Section of the International Society of Leather Trades' Chemists. The present volume contains these original papers, almost unchanged except by the addition of many unnecessary commas, and three new articles. This new material, not clearly indicated as such, consists of the papers by Cobb, by Hofmann, and by Werthan, and an index. The material written in 1934 has not been brought up

to date in subject matter or bibliographies, although there have been developments in these fields since that time.

Certain sections of this book may have interest and value for those working in biological fields. The first paper, "On the Mechanism of Emulsification" by Herbert Freundlich, deals with the production of emulsions by ultrasonic vibrations, and may interest those concerned with the physiological aspects of ultrasonics. The brief paper by Walsh and Frazer on "The Use of Highly Dispersed Emulsions in the Treatment of Toxaemic Conditions" should be of interest to readers of this journal, although it must be borne in mind that this paper was written in 1934. Two other papers deal with subjects related to the biological field, that by Corran on "Some Observations on a Typical Food Emulsion," namely mayonnaise and salad dressing, and that by Woodman on "Problems Connected with the Preparation and Application of Emulsions Used in Agricultural Spraying." The latter paper is long (43 pages); the author discusses various types of emulsions, their preparation, stability, and effect upon various insects and plants, and includes a 5 page bibliography.

Those interested in the preparation of emulsions will find the new article by Cobb on "The Fundamental Principles of Practical Emulsion Manufacture" to be specific and practical indeed. It should prove useful to any who may wish to make, alter, or keep an emulsion. The new paper by Hofmann on "Industrial Emulsion Formulation" is also specific and includes formulas for household and pharmaceutical products. The paper by R. I. Johnson on "The Design of Emulsifying Machines" contains descriptions of industrial emulsifiers of various types, all of large capacity, though mention is made of laboratory and hand type homogenizers.

The remaining articles deal with such subjects as paints, leather, and asphalt, and would appear to have little direct relation to the field of biology.

BELLE OTTO